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## An analysis of parasite communities of the Atlantic croaker, *Micropogonias undulatus* (Linnaeus), within the Chesapeake Bay

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AN ANALYSIS OF PARASITE COMMUNITIES OF  
THE ATLANTIC CROAKER, MICROPOGONIAS UNDULATUS  
(LINNAEUS), WITHIN THE CHESAPEAKE BAY.

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A Thesis

Presented to  
The Faculty of the Department of Marine Science  
The College of William & Mary in Virginia

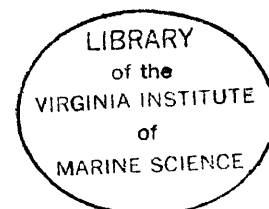
In Partial Fulfillment  
Of the Requirements for the Degree of  
Master of Arts

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by

David A. Benner

1980



## DEDICATION

This thesis is dedicated to my parents for all their support and encouragement that helped make this study possible.

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## ABSTRACT

This investigation analyzes the effects a migration from a coastal to an estuarine habitat has on the parasitocoenose of the Atlantic croaker, Micropogonias undulatus. A total of 502 fish were collected at monthly intervals from a sampling location near the mouth of the Chesapeake Bay and four sites on the York River. Fish were collected from July to October, 1977 and from April to October, 1978. Life history data collected on the croaker included age distribution within samples, gonadal maturation states, and frequency of occurrence of food items. Collected fish ranged from 73-451 mm TL representing 0+ to 3+ age classes. A Chi-square test with separate 2X2 contingency tables demonstrated that a significant difference existed between the frequency of 5 of 14 taxa reported as food items in large (>200 mm) and small (<200 mm) croakers. These taxa include: copepods, amphipods, brachyurans, osteichthyes, and pelecypods.

Twenty eight species of parasites, representing 8 new host and 10 new locality records, were recovered from the croaker. The new host records include the digenes Lepocreadium setiferoides, Stephanostomum tenue, Lecithochirium microstomum, Opecoeloides vitellus, and Cardicola sp.; the monogeneid Neopteriotrematoides avaginata; the nematode Goezia sp.; and the copepod Ergasilus labracis. Indices of diversity and dominance revealed that the parasitocoenose of the croakers entering the Bay in the spring was large in size but was dominated by the larval cestode, Tetraphyllidean sp. A. Species richness and equitability of the parasite community increased with the reduction of community size in collections taken later in the year. Cole's coefficient of association revealed neither a strong negative nor positive association existed between any two enteric helminths. A comparison of frequency of occurrence and levels of infection revealed no significant interspecific competition. The similarity of the parasite communities in host from separate geographical areas was shown to be different via Sorrenson's index and numerical classification. Numerical classification separated collections into 3 groups based on seasonality and size of the host. Parasites were placed into 6 species groups and interpreted via the two-way tables of nodal analysis. Differences in collection groups were shown to be due to shifts in species occurrences and abundances. The smaller croakers (<200 mm) were shown to possess parasite communities dominated by the acanthocephalan Dollfusentis chandleri and the monogeneid Absonifibula bychowski. Larger croakers (>200 mm) were separated into two groups by numerical classification based upon their parasite fauna. One group included fish collected in spring and early summer which possessed parasites believed to be acquired offshore. The other group included fish collected in late summer and fall which were characterized by parasite species believed to be acquired in the Bay. Although numerical classification forced collections of large croaker into two groups, the parasite fauna actually changed gradually through the summer.

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## INTRODUCTION

The purpose of this research project was to examine the parasite fauna of the Atlantic croaker, Micropogonias undulatus (Linnaeus), and to analyze what effect a migration from an oceanic to an estuarine habitat has on the parasitocoenose of fish of different sizes. The Atlantic croaker is a benthic euryhaline member of the sciaenid family that is generally regarded as a commercially important and valued game fish. The croaker ranges from the coastal waters of the Gulf of Maine to the western Gulf of Mexico (Welsh & Breder, 1923; Hildebrand & Cable, 1930; Chao, 1976). This fish is one of the most abundant inshore species found in the waters off the southeastern United States and is of sufficient commercial importance to be listed separately in the statistical catch reports of the National Marine Fisheries Service from all the border states extending from New York to Texas (Hildebrand & Cable, 1930; Bearden, 1964; Anderson, 1968).

The croaker is a migratory fish which enters the Chesapeake Bay in early spring and remains until late fall (Haven, 1957; Markle, 1976) at which time adults migrate out of the Bay to spawn offshore near its entrance (Haven, 1957). Croaker have an extended spawning season which begins in late summer and may continue into the early winter months (Welsh & Breder, 1923; Haven, 1957; Massman & Pacheco, 1960; Haven, 1957). It has also been postulated that postlarval croakers are carried up into the Chesapeake Bay by intruding saline bottom currents (Wallace, 1940). Catch statistics from winter surveys demonstrate that adults are taken

offshore while only first year juveniles are caught within the bay at that time (Welsh & Breder, 1923; Hildebrand & Schroeder, 1928; Raney & Massman, 1953; Massman, 1954; Massman & Pacheco, 1960; and Chao, 1976). The ability of juveniles to remain in the reaches of the bay and rivers during the winter suggests that younger fish may possess a greater tolerance to low temperature than adults. It is believed that the juveniles return to the sea with the rest of the migratory stock when they are approximately one year of age (Haven, 1957). White and Chittenden (1977) selected the 15th of October as the hatching date of the Atlantic croaker because this date is in the center of their extended spawning period. This date is contrary to the standard hatching date (January 1) used for fish north of Cape Hatteras (White & Chittenden, 1977). This unclear aspect in the life history of the Atlantic croaker has resulted in confusion concerning the population dynamics and biology of this fish.

Numerous studies have been conducted on the biology of M. undulatus. Food habit analyses reveal that this fish preys upon a wide variety of small fishes and marine invertebrates, predominantly small crustaceans, annelids and mollusks (Hildebrand & Schroeder, 1928; Roelofs, 1954; Overstreet & Heard, 1978). Overstreet and Heard (1978) also established that prey species consumed by the Atlantic croaker are directly related to the size of fish. Polyanski (1958) indicated that the parasite fauna of fish can be partly influenced by diet.

The amount of work done on the parasites and diseases of Micropogonias undulatus in northwest Atlantic coastal waters is minimal compared to the relatively high commercial interest in this fish species.

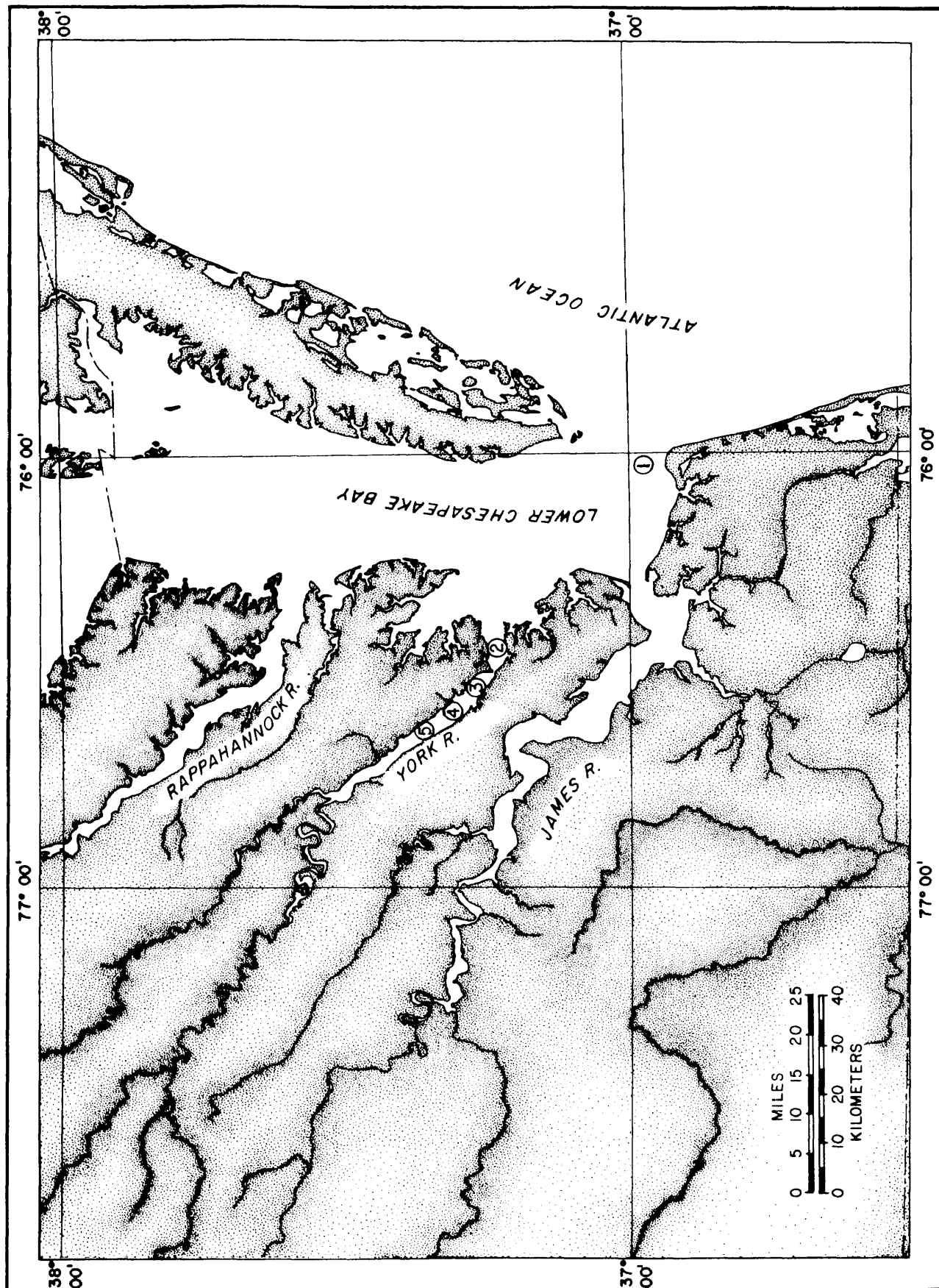
Overstreet (1972) stated that many of the parasite studies in the Chesapeake Bay and North Carolina area are outdated because the descriptions are insufficient by modern standards. The majority of parasitological work on the croaker has been reported from the estuarine and shelf areas of the Gulf of Mexico (Causey, 1953; Sogandares-Bernal, 1955; Hargis, 1956; Seamster & Monaco, 1956; Bullock, 1957; Wood & Mizelle, 1957; Sparks, 1958; Sparks & Thatcher, 1958; Overstreet, 1969; Overstreet, 1971; Joy, 1971; Joy, 1972; Overstreet, 1973; Joy, 1974; Norris & Overstreet, 1975; Lawler & Overstreet, 1976; Overstreet, 1977; Hendrix & Overstreet, 1977; Buckner et al. 1978). The recorded parasitological data from the croaker in Atlantic coastal waters are from earlier surveys of Linton (1905), Manter (1931, 1940), Pearse (1947, 1949), and more recently by Diaz & Johnson (1974). Parasitological research on the croaker within the Chesapeake Bay has been restricted to studies by O'Rourke (1949), Huizinga & Haley (1962), and Kingston et al. (1969).

### The Study Area

The Chesapeake Bay and its subestuaries comprise the largest estuarine system in the United States and has been classified by Pritchard (1967) as being moderately stratified. The relative volume of freshwater flow is balanced with the magnitude of tidal current. The major tributaries of the lower Chesapeake (Figure 1) are the James, York, and Rappahannock Rivers which together account for approximately 20% of the freshwater entering the Bay. The two geographical areas of interest for this study include the York River proper and the region of the Bay mouth.

The York River is formed by the confluence of the Pamunkey and Mattaponi Rivers about 50 km from the point of entry into the Chesapeake Bay. This river is tidal throughout its entire length and the 1.0 ‰ isohaline is normally 65-90 km from the mouth. The mean tidal range at the mouth is 0.7 m and the surface salinities range from 15-24 ‰ at this point. The recorded surface and bottom salinities are found normally to be within the mesohaline (5-18 ‰) category (Venice Hydrobiological Nomenclature, 1958) throughout the 40 km study area which extends upstream from the mouth. The surface and bottom temperatures in this area during the seven month (April-October) 1978 sampling period ranged from 17° to 28°C and 16° to 28°C, respectively (VIMS Crustaceology Hydrographic data). Surface and bottom river temperatures during the colder months are both normally reported to range between 2-5°C depending on the severity of the winter (VIMS Ichthyology Winter Trawl Survey data).

Figure 1. Location of sampling sites for Atlantic croakers captured at Chesapeake Bay mouth (1) and York River (2, 3, 4, 5).





Abnormally low water temperatures in the York River during several winters (1966-67; 1976-77; 1977-78) have been shown to be directly responsible for the decline in the catches of post-larval croakers and are postulated to be a contributing factor in the overall reduction of the commercial catch of Atlantic croakers in Virginia waters (Massman & Pacheco, 1960; Joseph, 1972; Wojcik, 1978). Wojcik (1978) states that bottom temperatures between  $2^{\circ}$  and  $2.5^{\circ}\text{C}$  alter the distribution of post-larval croakers throughout the river to a concentration at the mouth, and temperatures below  $1.5^{\circ}\text{C}$  results in total mortality.

The main body of the Chesapeake Bay lacks the heat storage capacity of the open ocean and as a result is generally colder in the winter and warmer in the summer. The mean surface and bottom temperatures of the water at the Bay mouth range from  $6-25^{\circ}\text{C}$  and  $6-16^{\circ}\text{C}$ , respectively (Beauchamp, 1974). The hydrographical characteristics of the Bay mouth region have been shown to be quite similar to nearby ocean waters but are significantly influenced by the outflow of freshwater. Mean sea surface salinity generally ranges between  $30^{\circ}/\text{oo}$  and  $33^{\circ}/\text{oo}$  except near the Chesapeake Bay entrance where values often drop at low as  $24^{\circ}/\text{oo}$ . The Bay entrance is also characterized by a sharp increase in salinity with depth. Subsurface tidal currents appear to be responsible for this distinct vertical salinity gradient. These currents are strong reversing tidal currents that exhibit a net outward flow at the surface and a net inward flow from mid-depth to the bottom. Beauchamp (1974) reports that the speed of the current flow at the surface and bottom of the water column in this region measured 1.2 and 0.9 knots during flood tide and 1.5 and 0.6 knots during ebb tide. Another current influential of the area is the Virginia Coastal Current, a surface current that flows southwest along the coast at an approximate rate of 0.6 knots.

## MATERIALS AND METHODS

### Fish Collection

A preliminary collection of adult and juvenile Micropogonias undulatus was conducted from July to October, 1977. Fish were collected in monthly samples from stations on the Rappahannock, James, and York Rivers. Partial results from the survey revealed that no gross differences existed in the parasite faunas from fish taken in the different rivers. This faunal similarity was attributed to the non-resident status of this species in the estuarine system and to the "relative" habitat similarity of the three rivers. A faunal difference was postulated to exist between the parasites acquired from the winter offshore habitat and those acquired from the estuarine habitat within the Chesapeake Bay. Thus, an ecological study was proposed to compare the parasites found associated with incoming and outgoing migratory croakers and to continuously monitor any faunal changes exhibited within this species during their seven month residence in the York River.

Samples of M. undulatus were collected from the incoming migratory stock near the Bay mouth during the months of April-May and from the outgoing stocks during September-October, 1978. A continuous monthly sampling program was conducted in the York River from May to October, 1978. Collection stations were located on the Cape Henry side of the Bay mouth (#1) and at five mile intervals on the York River (#2-4) (Figure 1).

Croakers collected at the bay station were captured by two separately owned commercial pound nets. The first set of nets was operated by A. Hudgins of Hampton and the other by T. Ross of Lynnhaven, Virginia. Fish samples were removed directly from the total catch in the vessel hold and in all cases were carefully checked for freshness.

Fish collected from the York River were obtained by a variety of methods. The most commonly used method was a 30' otter trawl equipped with a tickler chain. Tows were made at each station in both up and downstream directions for a duration of five minutes each. Additional croakers were obtained through the use of a 100' gill net with a 3" mesh. This net was set at dusk and fished the following morning using an 8' dingy. The remainder of the samples were obtained from a pound net operated by S. Hogge located at mile 5 on the river. All fish in each sample were placed into individual plastic bags and placed on ice before being transported to the Virginia Institute of Marine Science (VIMS). These bags ensured against the loss of voided parasites and cross contamination of ectoparasites during the trip to the laboratory.

#### Examination and Necropsy Procedures

Parasitic examinations are best done on freshly killed hosts but this was not always possible due to the limited seawater facilities at VIMS. The majority of iced fish were either necropsied or the essential organs and body parts were dissected out and fixed within 24 hours of collection. Total length (mm) and weight (gms) of each fish was recorded and scale samples were removed from the area immediately posterior to the pectoral fin just below the lateral line. The least degree of variation occurs in scales taken from this area (White & Chittenden, 1977). The

scales were pressed onto plastic cards and read according to the methodology established by White & Chittenden (1977). White & Chittenden (1977) selected October 15 as the hatching date of the Atlantic croaker due to the extended spawning period which can sometimes include two calendar years. The sex and gonadal condition of each fish was determined through the use of a field classification of the stages of sexual development established by Wallace (1940). The description of the gonads consisted of a total of eight stages ranging from immature to the rebuilding condition found after the ovary or testis has been spent. A total of only five stages were evident in the present investigation because croakers were not sampled during and after the period of actual spawning. The characteristics of each stage of sexual development are as follows:

Stage	<u>Female</u>	<u>Male</u>
Immature	Ovaries transparent yellow; round but thin; eggs undeveloped	Testis long thin strand; no development, flat, grayish in color
I	Ovaries small hard, pale yellow, eggs not distinguishable to naked eye	Testis narrow, triangular, hard; grayish
II	Ovaries 1/3 larger; eggs visible through membrane, faint blood vessels, more yellow	Testis 2X as large as previous stage; yellow-grey in color
III	Ovaries 3/4 full size; eggs clearly seen; numerous blood vessels; bright yellow	Testis wider, thicker, greasy in appearance; longitudinal striations whiter and softer than previous stage
IV	Ovaries swollen in body cavity; yellow-rose color; eggs loosely attached; blood vessels almost gone	Testis wide and soft; striations gone-filled out; milt and blood can be obtained by pressing sides of fish

V through VII      Spawning through recovery and rebuilding of gonads  
back to Stage I

Fish were necropsied according to the techniques of Amlacher (1961) and Hoffman (1967). A total of 101 croakers captured through July, 1978 were examined for blood parasites in smears prepared and fixed on ship-board. A complete absence of parasites in these smears resulted in the discontinuation of this procedure for the remainder of the investigation. A macroscopic examination was conducted for ectoparasites on the body surface and in the mouth cavity of each fish. A small portion of the fresh fish were examined for parasites while the majority had the alimentary tract and associated mesenteries removed and preserved in 10% neutral buffered formalin for later examination. In addition, the branchial baskets from these fish were removed and placed in a saturated hydrous chlorbutanol river water solution which, when shaken intermittently for one hour, has been shown to effectively relax the gill parasites in preparation for mounting and identification (Hargis, 1953). The fish examined without fixation allowed the recovery of living parasites which could be relaxed and flattened prior to fixation. Most helminths when killed by a fixative without flattening pressure contract severely and make identification quite difficult (Hoffman, 1967).

The body cavity and organs remaining after the removal of the alimentary tract were checked macroscopically for any evidence of parasites or pathology. The gall bladder was checked closely for the presence of myxosporidians. The number of each species of parasites was recorded and representative specimens were removed and prepared for mounting.

Parasite specimens removed live were relaxed in distilled water, fixed in hot AFA under coverslip pressure, and then either stored in a vial of 70% ETOH and glycerin with the remainder of the parasites from that host or were prepared for staining and mounting. Specimens fixed in situ were placed in a solution of approximately 0.25% of trisodium phosphate in distilled water to attain the proper degree of softness and pliability necessary for flattening (VanCleave & Ross, 1947). The details of the staining procedure varied according to the group of parasites. All Monogenea were processed according to the procedure of Dillon & Hargis (1966). Digenea, Aspidogastrea and Cestoda were prepared for study by following the procedures of Campbell (pers. comm.) except that Reynold's double stain was used in place of paracarmine. Acanthocephalans were processed according to the methods established by Bullock (1969). Nematodes were processed according to Meyer (1954) and temporarily mounted in lactic acid for identification. Parasitic crustacea were dissected and also temporarily mounted in the same manner as the nematodes except that permanent mounts were prepared with Hoyer's medium ringed with Zut.

In addition to the incidence and intensity of parasites, the frequency of occurrence of food items was recorded from the stomachs of the Atlantic croaker in two size groupings. The total length of 200 mm was selected as the separation point in the formation of size groups. The histograms presented by Chao (1976) demonstrated that 200 mm is the approximate maximum length that a juvenile croaker (spawned in early August and remaining in the Bay until late fall the following year) may achieve before migrating offshore. It was originally proposed that a separation be made based on age but this was considered unreasonable

for the following reasons: first, a large variation exists in length of fish in one age group due to the extended spawning period; Chao (1976) indicated that it was size that determines when juvenile croakers migrate out of the Bay for the first time; and, most importantly, the size of a fish and not its age has been shown to influence the diet. The organisms found as food items in this analysis were grouped into taxonomic categories that range from class to suborder.

### Statistical Analyses

A Chi-square test with separate 2X2 contingency tables (Tate & Clelland, 1959; Sokal & Rohlf, 1969) was employed to examine differences in the frequency of occurrence for each of the separate groupings of food items found in the stomach analyses. It was convenient to compute  $\chi^2$  from the 2X2 table through the formula:

$$\chi^2 = \frac{N(BC-AD - N/2)^2}{(A+B)(C+D)(A+C)(B+D)}$$

where A, B, C, and D are the observed frequencies in the upper left, upper right, lower left, and lower right cells, respectively, with N the total. Tate's correction for continuity is embodied in the formula through the subtraction of N/2 from the absolute value of BC-AD. Significance in this test results in the rejection of the null hypothesis that the frequency of a particular food item is the same in the two groups compared.

The remaining statistical analyses employed in the present investigation were used to elucidate the ecological relationships between parasites and better understand the prevalence and intensity of the parasitism. These ecological relationships were examined under the categories

diversity, dominance, association between individuals, and similarity of the parasite fauna between geographical areas.

Diversity indices were calculated using the equations from Margalef (1958) and Wilhm and Dorris (1968). The manner in which individuals are distributed among species in a community is reflected by community diversity ( $d$ ). This index expressed as "bits per fish" is a measure of complexity as well as the size of the parasite community. It is calculated by the equation:

$$d = \sum_{i=1}^S n_i \log_2 \frac{n_i}{n}$$

where  $n$  is the total number of individuals,  $n_i$  is the number of individuals of species  $i$  and  $s$  is the number of species per host. Community diversity values lie between a theoretical maximum diversity ( $d_{\max}$ ) and minimum diversity ( $d_{\min}$ ). Maximum diversity occurs if each individual belongs to a different species while minimum diversity occurs if all individuals of a community are of one species. These theoretical diversity indices are determined from the equations:

$$d_{\max} = \log_2 n! - s \log_2 \left(\frac{n}{s}\right)!$$

$$d_{\min} = \log_2 n! - \log_2 [n - (s-1)]!$$

A second index known as individual diversity ( $\bar{d}$ ) is the ratio of the number of individuals of each species to the total number of individuals. This index is independent of sample size and is calculated by the equation:

$$\bar{d} = \sum_{i=1}^S \frac{n_i}{n} \log_2 \frac{n_i}{n}$$



Unlike many general diversity indices,  $d$  and  $\bar{d}$  separate the ecological concept of diversity into two major components: equitability and species richness (Odum, 1971). A high  $d$  value is usually the result of a large and complex community while a high  $\bar{d}$  value is the result of complex organization within the community (Cloutman, 1975).

Dominance is another ecological concept which is important to this description of community structure. Odum (1971) defined an index of dominance as the summation of each species' importance in relation to the community as a whole. Redundancy ( $R$ ) is an expression of the dominance of one or more species, and is usually inversely related to individual diversity. It is calculated by the equation:

$$R = \frac{d_{\max} - d}{d_{\max} - d_{\min}}$$

In a parasite community, one parasite may influence the presence or absence of another, thus affecting community structure. Cole's coefficient of association (Cole, 1957) was used to determine whether a positive or negative relationship may exist between enteric helminths with greater than a 20% incidence. Cloutman (1975) defines a positive relationship as the presence of one parasite being advantageous to another or merely indicating that the parasites have mutual requirements. In contrast, a negative relationship may be due to interspecific competition or differences in environmental requirements. This coefficient was computed using a 2X2 contingency table and one of the following equations:

$$C_{AB} = \frac{f_{AB}}{Z_2 + f_{AB}} \quad \text{for a positive association } (f_{AB} = \frac{ad - bc}{N} > 0)$$

$Z_2$  = either a or d, whichever is smaller

or

$$C_{AB} = \frac{f_{AB}}{Z_1 - f_{AB}} \quad \text{for a negative association } (f_{AB} = \frac{ad - bc}{N} < 0)$$

$Z_1$  = either b or c, whichever is smaller

where a, b, c, d, are the observed frequencies in the upper left, upper right, lower left and lower right cells, respectively of the contingency table with N the total. The coefficient range extends from -1 to +1 with the coefficient equal to 0 when the number of joint occurrences equals the observed, +1 when the two species always occur together and -1 when the two species never occur together.

Possible association between helminth pairs was analyzed in terms of frequency of occurrence and levels of infection intensity. The helminth species were paired in 2X2 contingency tables under the categories of hosts infected with both, neither, and one to the exclusion of the other species. Frequency of occurrence was examined through the use of a Chi-square analysis (Sokal and Rohlf, 1969) that compared expected with observed values. Expected values for each level of association were calculated according to the formula of Tarwid (1960):

$$N_e = \frac{(Pa \times Pb)}{Nt}$$

where  $P_a$  and  $P_b$  are the frequency of occurrence of parasites  $a$  and  $b$  respectively, and  $N_t$  is the total number of hosts examined.

It was originally proposed that the mean levels of infection (mean worm burdens) for these enteric helminths be compared using a student's  $t$ -test, but the data did not meet the assumptions of this parametric test. Two nonparametric tests, the Mann Whitney  $U$ -test and the Wilcoxon two-sample test, were found to be suitable to compare the levels of infection. These tests are less powerful in their application since both pose the null hypothesis that the two samples come from populations having the same distribution. More specifically, if the ranks of the data from the two samples are significantly different then the null hypothesis that the samples have an equal location of distribution is rejected. The computational equations for these tests are the following:

when  $n_1 < 20$

$$c = n_1 n_2 + \frac{n_2 (n_2 + 1)}{2} - \sum_R^{n_2}$$

where  $U_s = C$  or  $(n_1 n_2 - C)$  whichever is greater

when  $n_1 > 20$

$$t_s = \frac{(U_s - \frac{n_1 n_2}{2})}{\frac{n_1 n_2 (n_1 + n_2 + 1)}{12}}$$

where  $n_1$  is the size of the larger sample and  $n_2$  is the size of the smaller,  $\sum_R^{n_2}$  is the sum of the ranks of the smaller sample, and  $U_2$  is the Mann-Whitney statistic. When  $n_1 < 20$  the Mann-Whitney  $U$ -test and the Wilcoxon two-sample test produce identical results. The test statistic  $U_s$  is also computed when  $n_1 > 20$  and is incorporated into the second equation which calculates a quantity that is approximately normally dis-

tributed and compared the critical value of  $t_{.05[\infty]}$  of a t-distribution.

The similarity of the parasite fauna recovered from different geographical areas was initially compared through the computation of Sorenson's index (Greig-Smith, 1964). This index reflects the qualitative similarity between two localities based on the number of species shared and the total number of species in each area. This index is defined by the equation:

$$S = (2C/A+B) \times 100$$

where A and B are the number of species in areas A and B, respectively, and C is the number of helminth species common to both areas. Similarity indices were computed and arranged in a trellis diagram for the categories of all parasites and Digenea only taken from fish greater than 200 mm. These results were then examined for trends in similarity.

The parasite data from the separate geographical sampling locations were also compared for similarity through the use of numerical classifications or cluster analysis. Numerical classification is defined as a wide variety of techniques that order entities into groups based on a set of algebraically expressed criteria or algorithms (Boesch, 1977). The chain of operations of this analysis began with the reduction of the original data matrix into a form which would permit the application of certain classification strategies and reduce the number of computations. Meristic data from all 502 croakers were initially reduced by the formation of 21 collection groups or stations. These groups were formed through the combined use of host size (greater or less than 200 mm), temporal intervals (11 months, 2 years) and location of capture

(Chesapeake Bay, York River). The exclusion criteria utilized for further reduction of data seemed to depend on the question being posed in the investigation and the nature of the ecological data. The lack of a significant number of hosts ( $<1.5\%$  of the total number of fish) lead to the elimination of 5 collection groups (Y831, Y841, Y872, Y761, Y772) while rare or poorly quantified species eliminated five parasites (Argulus bicolor, Clavella inversa, the microphallid digenes, the immature nematodes, and sanguinicolid digenes) from consideration in the numerical classification.

Ecological surveys, like the present investigation, often generate large data matrices which necessitate the use of a multivariate analytical technique like numerical classification. Boesch (1977) states these there is a tendency among those using numerical classification to casually subject these matrices to transformations without the proper consideration as to the nature of the data. He also warns that these data reductions, transformations and standardizations do have a profound effect on the results of the classification and should be used discretely.

Boesch (1977) states that transformation or standardization of the original data matrix is usually done when ecological collections produce large numbers of a few species or small numbers of many, the distribution of species abundance seems non-normal, or sampling effort is inconsistent. All of these criteria lead to the standardization of data by both collection and species total in the present investigation. Standardization is defined as an alteration depending on some property of the array of scores while transformation is an alteration of the attribute scores of entities. A collection total standardization is the computation of the

original species values as a percentage of the total ( $C.T.S. = \frac{X_i}{\sum X_i}$ ;  $X_i$  = importance of i-th species in a collection group). Standardization by species total results by dividing the species abundance values by the total abundance of the species in all collection groups ( $S.T.C. = \frac{X_i}{\sum X_j}$ ).

The next step in numerical classification is the selection and computation of a resemblance measure between all pairs of entities being classified. Boesch (1977) states that the selection of a resemblance measure is often based on convenience or because of precedent rather than rational criteria. The resemblance measure is a numerical expression of the degree of similarity or dissimilarity between the entities on the basis of their attributes. In this study, the entities are collection groups and attributes are the parasite species in a normal classification. An inverse classification utilizes species as entities with their presence in collection groups as attributes. The ecological questions posed by these two analyses are substantially different. The normal resemblance measure expresses the overall "likeness" between assemblages of organisms while the inverse reflects similarity in distribution patterns (spatial or temporal) between species. The Canberra-metric similarity coefficient was chosen for the analysis of the quantitative data in the present investigation because of the effect the size of the score has on this measure. An outstanding large attribute score does not dominate this coefficient, therefore inter-collection resemblance is based on the presence and numbers of all species. Similarity is expressed as a numerical value which is equal to one when the entities are identical and zero when the entities have no attributes in common.

Williams (1971) organized a classification of the variety of clustering methods and presented it in a dichotomized form. Boesch (1977) states that by far the most widely used clustering strategies are the methods included in the progression from exclusive to combinatorial categories. The respective characteristics of these categories include: a classification in which the entity may occur in only one group (exclusive), the formation of groups based solely on their attributes (intrinsic), the optimization of a route which begins with the progressive fusion of entities and ends with a complete population (hierarchical, agglomerative) and a variety of combinatorial strategies which can be used to compute group/group and group/entity resemblance measures from variants of a single linear equation (combinatorial).

Lance and Williams (1966, 1967) demonstrated a variety of combinatorial strategies that can compute resemblance measure from the equation  $D_{hk} = \alpha_i D_{hi} + \alpha_j D_{hj} + \beta D_{ij} + \gamma / (D_{hi} - D_{hj})$ . The two groups  $i$  and  $j$  fuse to form group  $k$  and the resemblance of group  $k$  to group  $h$  is computed as dissimilarity:  $D_{hi}$ ,  $D_{hj}$ ,  $D_{ij}$  to the total  $D_{hk}$ . The parameters  $\alpha_i$ ,  $\alpha_j$ ,  $\beta$  and  $\gamma$  determine the nature of the strategy. A flexible clustering strategy was chosen for the data in the present study under several constraints ( $\alpha_i + \alpha_j + \beta = 1$ ;  $\alpha_i = \alpha_j$ ;  $\beta = -0.25$ ;  $\gamma = 0$ ). The clustering coefficient  $\beta$  set at  $-0.25$  is an intensely clustering and moderately space dilating strategy. Agglomerations are made with a bias against an entity or group joining a large group and a bias in favor of entities or small groups forming separate branches of the hierarchy. This is an advantage in data sets where there is a high resemblance among common or abundant species and a lower resemblance among rarer species. Boesch (1977) stated that this clustering strategy with  $\beta$  set at  $-0.25$  has

produced satisfactory results in a wide range of data sets and has become conventional to this method of analysis. The disadvantage of this clustering method is that it is criticized for a loss in objectivity.

Sneath and Sokal (1973) claim that objectivity is decreased in flexible sorting because a cluster intensity is chosen that most closely fits preconceptions about the data.

Boesch (1977) states that the interpretation of the results of numerical classification can be greatly enhanced through the comparison of normal and inverse classifications and is greatly recommended as a routine post-clustering analysis. This ecological interpretation of the classifications can be accomplished by a two-way table of collection and species groups. The determination of these groups from the hierarchical classification was the second method considered to introduce subjectivity into the analysis. Branches of the dendrogram considered separate groups with reasonable internal resemblance were selected through the use of a variable stopping rule. This method allows the determination of "reasonable" groups without the stipulation that each group must be formed at a fixed level of resemblance. Boesch (1977) states that there is little justification for a stopping rule of fixed resemblance when inter-group and entity-group resemblance depends on the size of the group and when data sets include both ubiquitous and rare species. Groups of ubiquitous species will demonstrate a higher intra-group resemblance than those of rare species in which the probability of co-occurrence is low.

The two-way tables of the selected groups reveal differences in collection groups based on the frequency of members in species groups and differences in the distribution pattern of species groups based on



the abundance of species in various collection groups. Williams and Lambert (1961) termed this approach "nodal analysis" since one attempts to describe and interpret dense cells of the data matrix in which a group of species and group of collections coincide. These comparisons are interpreted through the ecological concepts of constancy, fidelity and dominance.

Constancy is defined as the number of occurrences of species in a collection group divided by the total possible number of occurrences. This concept is expressed as a percentage and computed by the equation:

$C_{ij} = A_{ij} / (n_i n_j)$  where  $A_{ij}$  = actual number of occurrences of species group  $i$  in collection group  $j$  and  $n_i n_j$  = the number of entities in

respective groups. The concept of fidelity is the degree to which species select or are limited to collection groups. It is represented by cell fidelity which is the constancy of species to a collection group divided by constancy over all collections and cell fidelity Chi-square which is the comparison of observed and expected values. Fidelity was

computed by the equation: 
$$F_{ij} = \frac{(A_{ij} \sum_j n_j)}{(N_j \sum_j A_{ij})}$$
 with  $A_{ij}$  = defined previously;

$\sum_j n_j$  - sum of the number of entities in collection group  $j$ ;  $n_j$  = number entities in collection group  $j$ ;  $\sum_j A_{ij}$  = sum of the actual number of occurrences of species group  $i$  in collection group  $j$ . The remaining two-way table is an abundance matrix which represents the average abundance in a collection group divided by the average overall abundance.

The effect of parasitism on the condition (degree of robustness) or health of a fish was determined according to the methods of Lagler (1952). A condition coefficient ( $K$ ) was computed for all juvenile fish less than

200 mm infected with D. chandleri and compared to the condition factor of all uninfected fish of the same size by using a t-test (Sokal & Rohlf, 1969). This condition coefficient is defined by the equation:

$$K = \frac{10^5 W}{L^3}$$

where W = width of the fish and L = length. The criteria necessary for the correct use of this coefficient lead to its use only on juvenile fish less than 200 mm in length. The use of the coefficient on larger fish mandates that the fish be captured at the same time and be of the same sex, spawning condition, and age. The acanthocephalan, D. chandleri, was chosen as the parasite of study because of its high incidence in small croakers and its documented reputation for causing pathology.

## RESULTS

### Fish Samples

The number, age, size, and sex of fish examined each month from the two sampling locations are listed in Table 1. A total of 101 M. undulatus were collected during the 1977 preliminary York River survey while a total of 401 croakers were collected in 1978. Examination of Table 1 reveals that a total of 130 migrating croakers was captured at the Chesapeake Bay mouth station while a total of 206 fish in the 1+ age class or older was collected during the 7 month sampling period in the York River. The remaining 166 fish included in the sample are the 0+ age class croakers which have been shown to migrate into the bay and remain there for their first year. Table 1 demonstrates that a large difference exists in the numbers of collected fish of each sex as well as the number of fish taken monthly in the size categories presented in the following section.

### Stomach Contents

A total of 307 of 502 fish was found to contain one or more of the sixteen different groups of food items presented in Table 2. This table separates fish into the two size categories of less than or greater than 200 mm. It is apparent from this data that small croakers (77-199 mm) primarily consumed large quantities of polychaetes, and total crustaceans. The crustaceans in this case consisted mainly of mysids (33.0%), copepods (42.3%), amphipods (39.2%), and isopods (19.6%). All four groups of these crustaceans were found to decrease in number considerably in the successive size category. Carideans appeared to make up a small but consistent

Table 1. Monthly sample of croakers by age, sex and total length.

	Age				Sex (Total No.'s)		Total Length (mm)	
	0+	1+	2+	3+			<200	>200
1977								
Yrk. Rvr.								
July	-	21	9	1	22	9	-	31
August	8	9	1	-	12	6	8	10
September	11	3	-	-	6	8	6	8
October	37	1	-	-	16	22	37	1
TOTAL	56	34	10	1	56	45	51	50
1978								
Ches. Bay								
April	-	19	30	1	49	1	-	50
May	-	1	18	1	17	3	-	20
September	-	17	12	1	24	6	-	30
October	-	18	1	1	25	5	-	30
TOTAL	-	55	71	4	115	15	-	130
1978								
Yrk. Rvr.								
May	-	4	6	-	7	3	-	10
June	1	18	32	-	34	17	1	50
July	2	36	14	-	28	24	2	50
August	19	18	22	-	36	23	19	40
September	88	4	6	-	56	42	81	17
October	-	-	1	-	1	-	-	1
TOTAL	110	80	81	0	162	109	103	168
Cumul.								
Total	177	169	162	5	333	169	154	348

Table 2. Stomach contents of the Atlantic croaker.

Fish Length (mm)	73-199		>200	
No. Fish Examined	154		348	
No. Fish w/Food	97		210	

Food Organism or Material	No. Fish	% Occurrence	No. Fish	% Occurrence
Pelecypoda	7	7.2	91	43.3
Polychaetea	15	15.4	40	19.0
Ostracoda	3	3.1	2	1.0
Copepoda	41	42.3	3	1.4
Cirripedia	-	0.0	3	1.4
Mysidacea	32	33.0	24	11.4
Amphipoda	38	39.2	7	3.3
Isopoda	19	19.6	5	2.4
Caridea	5	5.2	12	5.7
Brachyura	2	2.1	71	33.8
Asciadiacea	-	0.0	4	1.9
Osteichthyes	2	2.1	99	47.1
Cumacea	1	1.0	-	0.0
Gastropoda	2	2.1	1	0.5
Detritus	4	4.1	14	6.7
Sediment	3	3.1	8	3.8

portion of the croaker diet in both size categories. It was found that even though penaeids and carideans exist in the Chesapeake Bay area, very few croakers utilized these shrimp as a food source. The percentage of polychaetes in the diet remained relatively consistent in all size classes. The food item groupings of pelecypods, brachyurans, and osteichthyes increased in importance in large fish.

A Chi-square test with Yates correction for continuity demonstrated that the following food items were significantly different at the 0.1 level (Table 3) in fish less than 200 mm and those greater than 200 mm: amphipods, copepods, brachyurans, pelecypods, and osteichthyes. The cumulative frequencies of all food items presented in Table 3 demonstrates that these five food groupings in terms of frequency comprise a major portion of the croaker diet. Copepods and amphipods account for 45.4% of the diet of croakers less than 200 mm while pelecypods, brachyurans and osteichthyes account for 68.0% of the diet of larger size croakers.

#### Age and Growth

The age, sex, and size range of all fish samples in this investigation are presented in Table 4. These data reveal an overlap in the fish lengths between age classes as well as a large difference in the number of captured female vs. male fish. The overall size range is shown to vary from a 73 mm young of the year to a 451 mm adult which was computed to be approaching four years of age. Female fish are shown to comprise nearly 3/4 (74.7%) of the total number of fish collected in the 1+ to 3+ age categories and were generally larger in size than in the 1+ and 2+ age categories.

Table 3. Chi-square values and the cumulative frequency of food items in different size croakers.

Food Item or Material	Chi-square Value	Cum. Freq. Fish <200 mm	Cum. Freq. Fish >200 mm
Pelecypoda	2.74*	4.0	23.7
Polychaetea	0.03	8.6	10.4
Ostracoda	0.08	1.7	0.5
Copepoda	3.91*	23.6	0.8
Cirripedia	0.10	0.0	0.8
Mysidacea	0.90	18.4	6.2
Amphipoda	3.07*	21.8	1.8
Isopoda	1.20	10.9	1.3
Caridea	0.01	2.9	3.1
Brachyura	2.72*	1.2	18.5
Ascidacea	0.14	0.0	1.0
Osteichthyes	4.35*	1.2	25.8
Cumacea	0.01	0.5	0.1
Gastropoda	0.07	1.2	0.3
Detritus	0.05	2.3	3.7
Sediment	0.01	1.7	2.1
		<u>100.0</u>	<u>100.0</u>

\*Significant at 0.1 level.

Table 4. Age, sex, and size range of all Atlantic croaker.

Age class	0+	1+	2+	3+
Size range (mm)	73-218	193-337	280-420	415-451
Sex-male	91	115	130	5
Sex-female	75	51	35	0
Total number	166	167	164	5
Mean length (mm)	145.1	275.8	336.7	-
Mean length (mm)	151.6	269.9	325.3	-
Mean length (mm) of both sexes	148	274	334	423



### Sex of Fish

Numbers of each sex in each age group of croakers are separated into gonadal classification stages in Table 5. In general, the mature fish captured in the earlier months of the present survey exhibited low gonadal indices while those captured later in the summer demonstrated maturing or rebuilding gonads representing higher indices. The smallest mature male croaker was 263 mm in length and was captured in September. A total of 31.4% of the male croakers matured before 2 years of age. In contrast, no female croaker matured until the third year of growth. The smallest mature female was 287 mm in length and was captured in June.

### Parasites

Phylum Platyhelminthes  
Class Trematoda  
Subclass Digenea  
Family Lepocreadiidae

Lepocreadium setiferoides (Miller and Northrup, 1926) has been previously reported as an adult intestinal parasite of the summer flounder, Paralichthys dentatus. The occurrence of L. setiferoides in M. undulatus is considered a new host record. Lepocreadium micropogoni has been reported from the Atlantic croaker in the coastal waters of North Carolina by Pearse (1949) but the validity of this report has been questioned in the literature. It is postulated that L. micropogoni may have been a misidentification of L. setiferoides.

Lepocreadium setiferoides was found in the intestine of 122 of 502 (24.3%) croakers collected in the present investigation. The number of individuals ranged from 1 to 68 with a mean intensity of 7.2 parasites per fish. An increasing trend in the incidence and intensity of L. setiferoides is evident in the data presented in Table 6. This digene

Table 5. Relationship of the age of croakers to sexual maturity.

Age in Years	Percentage of Females in Maturity Stages					Total No. of Fish
	Immature	I	II	III	IV	
0+	100.0	0.0	0.0	0.0	0.0	91
1+	100.0	0.0	0.0	0.0	0.0	115
2+	0.0	39.5	23.8	30.8	6.9	130
3+	0.0	40.0	20.0	20.0	20.0	5

Age in Years	Percentage of Males in Maturity Stages					Total No. of Fish
	Immature	I	II	III	IV	
0+	100.0	0.0	0.0	0.0	0.0	75
1+	68.6	21.6	7.9	1.9	0.0	51
2+	0.0	20.0	60.0	14.3	5.7	35
3+	0.0	0.0	0.0	0.0	0.0	0

263 mm smallest mature male  
 287 mm smallest mature female

Table 6. Infection incidence and intensity of Lepocreadium setiferoides

Chesapeake Bay (>200 mm)		York River (>200 mm)			York River (<200 mm)		
Infect/	Incid.	Mean	Range	Infect/	Incid.	Mean	Range
Total No.	(%)	Inten.		Total No.	(%)	Inten.	
1977							
July				3/31	9.7	7.3	2-18
Aug.				3/10	30.0	2.7	2-4
Sept.				2/8	25.0	1.5	1-2
Oct.				0/1	-	-	-
1978							
April	0/50	-	-				
May	0/20	-	-	7/10	70.0	4.4	1-11
June				31/50	62.0	13.1	1-68
July				19/50	38.0	10.3	1-51
Aug.				19/40	47.5	5.3	1-59
Sept.	16/30	53.3	9.3	8/17	80.0	5.4	1-15
Oct.	6/30	20.0	10.6	0/1	-	-	-

Total\*

In 0/70 0.0 - -

Total\*

Out 22/60 36.7 - -

1977

1978

Cumul.

Total

8/50 16.0 - - 4/51 7.8 - -  
84/158 50.0 - - 4/103 3.9 - -  
88/218 42.2 - - 8/153 4.6 - -

\*Total fish captured at Chesapeake Bay mouth station (In = April and May) (Out = Sept. and Oct.)

was absent in croakers sampled at the Chesapeake Bay mouth during the spring migration of this fish from offshore winter habitat into the estuary. It appeared in 42.2% of the York River samples and remained at this approximate level of infection (36.7%) in croakers migrating out of the bay in the fall. It should be noted that this digene occurred in only 4.5% of the croakers less than 200 mm in length.

#### Family Acanthocolpidae

Stephanostomum tenue (Linton, 1898) was previously reported from a variety of piscine hosts but has been found most often in the striped bass, Morone saxatilis (Martin, 1939). This digene has been previously reported in the Chesapeake Bay as an intestinal parasite of the striped bass by Paperna and Zwerner (1976).

Stephanostomum tenue was recovered from the intestine of 80 of 502 (15.9%) M. undulatus collected during the present investigation. The number of individuals ranged from 1 to 112 with a mean intensity of 5.2 parasites per fish. An increasing trend in the incidence and intensity of S. tenue is evident in the data presented in Table 7. This digene was absent in the migratory croakers captured in the spring, increased to an incidence of 22.0% in fish captured in the York River, and was found in 53.0% of the croakers moving offshore to spawn. Stephanostomum tenue was not reported from croakers less than 200 mm in length.

#### Family Hemiuridae

Lecithochirium microstomum Chandler, 1935 is a parasite in the stomach of fishes. Reports of this parasite range from North Carolina to Louisiana and the Galapagos Islands. The nearest geographical occurrence of this parasite is from Beaufort, N.C. in Galeichthys milberti. The

Table 7. Infection incidence and intensity of Stephanostomum tenue

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range
1977												
July					11/31	35.5	2.6	1-6				
Aug.					1/10	10.0	1.0	-	0/8	-	-	-
Sept.					1/8	12.5	3.0	-	0/6	-	-	-
Oct.					0/1	-	-	-	0/37	-	-	-
1978												
April	0/50	-	-	-								
May	0/20	-	-	-	0/10	0.0	-	-				
June					4/50	8.0	3.5	1-6	0/1	-	-	-
July					4/50	8.0	1.5	1-2	0/2	-	-	-
Aug.					19/40	47.5	5.5	1-17	0/19	-	-	-
Sept.	17/30	56.7	8.9	1-112	8/17	47.1	4.2	1-15	0/81	-	-	-
Oct.	15/30	50.0	4.9	1-22	0/1	-	-	-				
Total												
In	0/70	0.0	-	-								
Total												
Out	32/60	53.3	-	-								
1977					13/50	26.0	-	-	0/51	-	-	-
1978					35/168	20.8	-	-	0/103	-	-	-
Cumul.												
Total					48/218	22.0	-	-	0/154	-	-	-

occurrence of this digene in the present investigation is a new host and locality record.

Lecithochirium microstomum was found in the stomach of only 4 of 502 (<1.0%) M. undulatus examined in the present investigation. The number of individuals ranged from 1 to 3 with a mean intensity of 1.8 parasites per fish. All specimens of this digene were recovered from croakers captured at the Bay mouth during the spring migration into the Bay.

Two different unidentifiable hemiurid species were recovered in the present investigation and are referred to as species "A" and "B". Species "A" is a mature digene which was found in 18 of 502 (3.6%) Atlantic croakers. This species is a large heavy-bodied digene which when fixed in situ resulted in extensive contraction and distortion. Identification to the generic level was not possible due to the inability to observe the terminal genitalia. The number of individuals ranged from 1 to 4 with a mean intensity of 1.3 parasites per fish. The data presented in Table 8 demonstrate that this digene is found in croakers throughout the sampling period.

Species "B" is an immature digene which was found in only 2 of 502 (<1.0%) Atlantic croakers. The intensity of infection was significantly less than species "A" with only a total of 3 specimens recovered from fish captured at the Chesapeake Bay mouth in May and the York River in June.

#### Family Opecoelidae

Two opecoelid species recovered in the present investigation have

Table 8. Infection incidence and intensity of Hemiurid Species "A"

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Inten. (%)	Mean Range	Infect/ Total No.	Incid. (%)	Inten. (%)	Mean Range	Infect/ Total No.	Incid. (%)	Inten. (%)	Mean Range
1977												
July					1/31	3.2	1.0	-				
Aug.					0/10	-	-	-	0/8	-	-	-
Sept.					0/8	-	-	-	0/6	-	-	-
Oct.					0/1	-	-	-	0/37	-	-	-
1978												
April	4/50	8.0	1.5	1-2								
May	2/20	10.0	2.0	1-3	1/10	10.0	4.0	-				
June					3/50	6.0	1.0	-	0/1	-	-	-
July					3/50	6.0	1.0	-	0/2	-	-	-
Aug.					1/40	2.5	1.0	-	0/19	-	-	-
Sept.	0/30	-	-	-	1/17	10.0	1.0	-	0/81	-	-	-
Oct.	0/30	-	-	-	1/1	100.0	1.0	-				
Total												
In	6/70	8.6	-	-								
Total												
Out	0/60	-	-	-								
1977												
1978					1/50	2.0	-	-				
					10/168	6.0	-	-				
Cumul.												
Total					11/218	6.1	-	-				

been shown to occur in the same host but in different locations. Opecoeloides fimbriatus (Linton, 1900) is thought to occur mostly in the pyloric caeca and intestine while Opecoeloides vitellosus (Linton, 1934) primarily occupies the rectum (Overstreet, pers. comm.).

Opecoeloides fimbriatus has been reported from a variety of piscine hosts which range geographically from the coastal waters of New England to the Gulf of Mexico. This digene has been reported from M. undulatus in the Gulf of Mexico by Sparks (1958). Opecoeloides fimbriatus was by far the most abundant of the two opecoelid species in the present study. It was found in 81 of 502 (16.1%) M. undulatus examined during the present study. The number of individuals ranged from 1 to 12 with a mean intensity of 2.3 parasites per fish. The seasonal incidence and intensity data are presented in Table 9. Examination of the data demonstrates a decreasing trend of incidence with an infection of 41.4% in spring migratory fish to 17.9% and 16.6% incidence of infection in York River fish and fall migratory croakers, respectively. The incidence in fish less than 200 mm in length was only 1.9% for both sampling years.

Opecoeloides vitellosus, like O. fimbriatus, has been reported from several piscine hosts that range from New England to the Gulf of Mexico. The occurrence of O. vitellosus in the croaker of the Chesapeake Bay area represents a new host and locality record for this parasite. This digene was recovered from 21 of 502 (4.2%) M. undulatus during the present investigation. The number of individuals ranged from 1 to 4 with a mean intensity of 1.4 parasites per fish. Table 10 includes seasonal data which indicate a decreasing trend in the incidence of this digene in the Atlantic croaker. Opecoeloides vitellosus was recovered in 8.0% of the



Table 9. Infection incidence and intensity of Opecoeloides fimbriatus

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range
1977												
July					4/31	13.3	1.3	1-2				
Aug.					0/10	-	-	-	0/8	-	-	-
Sept.					2/8	25.0	1.0	-	0/6	-	-	-
Oct.					1/1	100.0	2.0	-	1/37	2.7	1.0	-
1978												
April	19/50	38.0	2.2	1-7								
May	10/20	50.0	3.1	1-8	4/10	40.0	1.8	1-2				
June					11/50	22.0	3.1	1-12	0/1	-	-	-
July					10/50	20.0	2.3	1-9	0/2	-	-	-
Aug.					3/40	7.5	1.0	-	2/81	2.5	1.0	-
Sept.	4/30	13.3	1.3	1-2	3/17	17.6	1.0	-				
Oct.	6/30	20.0	3.2	1-12	1/1	100.0	6.0	-				
Total												
In	29/70	41.4	-	-								
Total												
Out	10/60	16.6	-	-								
1977					7/50	14.0	-	-	1/51	2.0	-	-
1978					32/168	19.0	-	-	2/103	2.3	-	-
Cumul.												
Total					39/218	17.9	-	-	3/154	1.9	-	-

Table 10. Infection incidence and intensity of Opecoeloides vitellosus

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Inten. Mean	Range	Infect/ Total No.	Incid. (%)	Inten. Mean	Range	Infect/ Total No.	Incid. (%)	Inten. Mean	Range
1977												
July					0/31	-	-	-	0/8	-	-	-
Aug.					0/10	-	-	-	0/6	-	-	-
Sept.					0/8	-	-	-	0/37	-	-	-
Oct.					0/1	-	-	-				
1978												
April	0/50	-	-	-								
May	6/20	30.0	1.0	-	2/10	20.0	1.0	-				
June					4/50	8.0	1.5	1-3	0/1	-	-	-
July					4/50	8.0	2.0	1-4	0/2	-	-	-
Aug.					2/40	5.0	1.0	-	0/19	-	-	-
Sept.	2/30	6.7	1.0	-	0/17	-	-	-	0/81	-	-	-
Oct.	1/30	3.3	1.0	-	0/1	-	-	-				
Total												
In	8/70	8.5	-	-								
Total												
Out	3/60	5.0	-	-								
1977					0/50	-	-	-	0/51	-	-	-
1978					12/168	7.1	-	-	0/103	-	-	-
Cumul.												
Total					12/218	5.5	-	-	0/154	-	-	-

incoming migratory fish in the spring, 5.5% of the York River fish, and 5.0% of the croakers migrating out to sea to spawn in the fall. It should be noted that this parasite was not present in croakers less than 200 mm in length.

#### Family Monorchidae

Diplomonorchis leiostomi Hopkins, 1941 is a tiny oval-shaped digene found primarily in the intestine and pyloric ceca of the host. It was originally described from Leiostomus xanthurus and Orthopristis chrysopterus in Beaufort, N.C. by Hopkins (1941a). Since that time it has been reported from a variety of hosts in the Gulf of Mexico. These reports include Micropogonias furnieri from Jamaica by Nahhas & Cable (1964) and Micropogonias undulatus from the coastal waters of Florida by Nahhas & Powell (1965). The recovery of this digene in the present study represents a new locality record.

Diplomonorchis leiostomi was found in 163 of 502 (32.5%) M. undulatus collected during the present investigation. The number of individuals ranged from 1 to 1505 with a mean intensity of 23.4 digenes per fish. This mean intensity is somewhat misleading due to the enormous number of this parasite recovered from one fish. Seasonal incidence and intensity data are presented in Table 11. Examination of these data reveals that infections in adult croakers did not change over the seven month sampling period. The incidence of infection in croakers less than 200 mm in length was found to be 20.1%.

#### Family Microphallidae

Adult members of the Microphallidae are primarily intestinal parasites of birds with a few species occurring in fishes and mammals

Table 11. Infection and incidence and intensity of Diplomonorchis leiostomi

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Inten. Mean	Range	Infect/ Total No.	Incid. (%)	Inten. Mean	Range	Infect/ Total No.	Incid. (%)	Inten. Mean	Range
1977												
July					8/31	25.8	2.5	9-5				
Aug.					7/10	70.0	5.3	1-12	1/8	12.5	1.0	-
Sept.					4/8	50.0	5.1	1-7	2/6	33.3	4.0	-
Oct.					0/1	-	-	-	4/37	10.8	2.5	-
1978												
April	10/50	20.0	4.0	1-15								
May	1/20	55.0	11.5	1-56	6/10	50.0	17.0	1-54	1/1	100.0	7.0	-
June					27/50	54.0	22.5	1-201				-
July					15/50	30.0	12.9	1-28	0/2	-		-
Aug.					22/40	55.0	10.0	1-116	3/19	15.7	1.3	1-2
Sept.	5/30	16.7	12.8	1-41	9/17	52.9	45.5	1-282	20/81	24.5	4.8	1-29
Oct.	10/30	33.3	200	1-1505	0/1	-	-	-				
Total												
In	21/70	30.0	-	-								
Total												
Out	15/60	25.0	-	-								
1977					19/50	38.0	-	-	7/51	13.7	-	-
1978					79/168	47.0	-	-	24/103	23.3	-	-
Cumul.												
Total					98/218	45.0	-	-	31/154	1.9	-	-

(Schell, 1970). Specimens of an immature microphallid were found in the intestine of 4 Atlantic croakers captured in June, 1978. The number of individuals ranged from 1-5 with a mean intensity of 2.3 parasites per fish. In all cases, gonadal products were absent in the specimens of this trematode. The occurrence of nonfunctional gonads suggests that M. undulatus may serve as a paratenic or transfer host for this digene. Due to the lack of quality specimens, it can only be postulated that this microphallid belongs in one of two genera: Microphallus or Megalophallus. Both genera possess species which have been reported in the Chesapeake Bay-Beaufort area as metacercariae in the blue crab, Callinectes sapidus, and as adults in an avian definitive host.

#### Family Sanguinicolidae

The digenes that make up the family Sanguinicolidae parasitize the circulatory system of their hosts (Yamaguti, 1958). These trematodes do not represent typical examples of the digenea because the sanguinicolids possess a life cycle which includes only one intermediate host, lacks the characteristic suckers, and are collected most often from the heart or branchial arteries of the host. Specimens of an unidentified species of Cardicola were recovered from the drained blood of the branchial arteries in 13 of 502 (2.6%) M. undulatus captured in April and May, 1978 at the Chesapeake Bay mouth station and during June and July, 1978 in the York River. This incidence data is considered incomplete because not all of the collected fish were specifically examined for this parasite. There are no reports of a species of Cardicola from the croaker or for that matter any fish captured in the western Atlantic. The occurrence of this digene represents not only a new host and locality record for this genus but it is believed that it may also be a new species.

Subclass Monogenea  
Family Macrovalvitrematidae

Macrovalvitrematoides micropogoni (Pearse, 1949; Hargis, 1956) is an ectoparasite first reported from the gills of M. undulatus in Beaufort, N.C. It ranges from the western Gulf of Mexico to the Chesapeake Bay and is host specific for the Atlantic croaker.

Macrovalvitrematoides micropogoni was found on the gills of 362 of 502 (72.1%) M. undulatus collected during the present investigation. The number of individuals ranged from 1-60 with a mean intensity of 4.5 monogenes per fish. Seasonal incidence and intensity data are presented in Table 12. Examination of this table reveals that the highest incidence of infection occurred in adult fish captured in the York River. Both the incoming and outgoing fish had a lower incidence of infection. Croakers less than 200 mm in length had a high prevalence of infection at 69.1%. Macrovalvitrematoides micropogoni was often found with another monogeneid, Neopteriotrematoides avaginata.

Neopteriotrematoides avaginata, Suriano, 1975 is the monotypic representative of this genus which was erected through the study of specimens taken from the gills of Micropogonias furnieri captured in the coastal waters off Brazil. The occurrence of this monogeneid on M. undulatus in the Chesapeake Bay is a new host and locality record.

Neopteriotrematoides avaginata was found on the gills of 186 of 502 (37.0%) M. undulatus collected during the present investigation. The number of individuals ranged from 1 to 71 with a mean intensity of 4.4 monogeneids per fish. Table 13 includes seasonal data which indicates a definite decreasing trend in the incidence of this monogeneid in the

Table 12. Infection incidence and intensity of Macrovalvitrematoides micropogoni

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incident. (%)	Inten. Mean	Range	Infect/ Total No.	Incident. (%)	Inten. Mean	Range	Infect/ Total No.	Incident. (%)	Inten. Mean	Range
1977												
July					29/31	93.5	6.7	1-18				
Aug.					8/10	80.0	3.5	1-8	6/8	75.0	2.3	1-8
Sept.					8/8	100.0	3.0	1-4	2/6	33.0	3.6	1-8
Oct.					1/1	100.0	1.0	-	20/37	54.0	2.2	1-5
1978												
April	34/50	68.0	4.0	1-10								
May	6/20	30.0	4.0	1-7	7/10	70.0	2.7	1-6	0/1	-	-	-
June					44/50	88.0	5.1	1-60				
July					48/50	96.0	5.8	1-16	2/2	100.0	1.0	-
Aug.					24/40	60.0	4.8	1-22	14/19	73.7	3.3	1-9
Sept.	17/30	56.7	2.2	1-6	11/17	64.7	6.0	1-13	60/81	74.1	3.8	1-19
Oct.	23/30	76.7	7.4	1-18	1/1	100.0	1.0	-				
Total												
In	40/70	57.1	-	-								
Total												
Out	40/60	66.7	-	-								
1977					46/50	92.0	-	-	28/51	64.7	-	-
1978					135/168	80.4	-	-	76/103	73.8	-	-
Cumul.												
Total					181/218	83.0	-	-	104/154	70.8	-	-

Table 13. Infection incidence and intensity of *Neopterinothrematoidea avaginata*

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/	Incid.	Inten.	Range	Infect/	Incid.	Inten.	Range	Infect/	Incid.	Inten.	Range
	Total No.	(%)			Total No.	(%)			Total No.	(%)		
1977												
July					19/31	61.3	2.8	1-7				
Aug.					5/10	50.6	3.0	1-5	1/8	12.5	3.0	-
Sept.					3/8	37.5	1.0	-	1/6	16.7	2.0	-
Oct.					0/1	-	-	-	2/37	5.4	1.5	1-2
1978												
April	46/50	92.0	8.1	1-27								
May	5/20	25.0	2.8	2-4	7/10	70.0	4.6	2-7				
June					30/50	60.0	4.0	1-32	0/1	-	-	-
July					31/50	62.0	2.2	1-6	0/2	-	-	-
Aug.					4/40	10.0	1.5	1-2	3/19	-	-	-
Sept.	5/30	16.6	1.0	-	2/17	20.0	2.5	1-4	12/81	14.8	1.2	1-2
Oct.	12/30	40.0	8.0	1-71	0/1	-	-	-				
Total												
In	51/70	72.8	-	-								
Total												
Out	17/60	28.3	-	-								
1977					27/50	54.0	-	-	4/51	7.8	-	-
1978					74/168	44.0	-	-	15/103	14.6	-	-
Cumul.												
Total					101/128	46.3	-	-	19/154	12.3	-	-



Atlantic croaker, Neopteriotrematoides avaginata was recovered in 72.8% of incoming migratory fish in the spring, 46.3% of the York River fish and 28.3% of the croakers leaving the Bay to spawn. The incidence of infection was 12.3% for fish less than 200 mm in length.

#### Family Diclidophoridae

Absonifibula bychowski Lawler and Overstreet, 1976 is the monotypic representative of this genus which was originally described from specimens taken from Atlantic croakers captured in the Gulf of Mexico. The occurrence of this monogeneid in the Chesapeake Bay area represents a new locality record.

Absonifibula bychowski was recovered in the present investigation from only 7 of 502 (1.4%) M. undulatus. All of the infected hosts were captured in the York River (Oct, 1977; Sept. 1978), were less than 200 mm in length, and were considered to be young of the year. The number of individuals ranged from 1 to 2 individuals with a mean intensity of only 1.3 monogeneids per fish. The total incidence of infection in fish less than 200 mm was 4.6%.

#### Subclass Aspidogastrea Family Aspidogasteridae

Lobatostoma ringens (Linton, 1907) Eckmann, 1932, is a parasite of teleosts and lamellibranchs that has been reported in the literature more often than any other marine aspidogastrid (Hendrix and Overstreet, 1977). It was originally described by Linton (1905) from M. undulatus captured in Beaufort, North Carolina. Since that time, this parasite has been reported from hosts ranging from the coastal waters of Virginia to Argentina (Yamaguti, 1963a).

Lobatostoma ringens was found in the intestine of 256 of 502 (51.0%) M. undulatus collected during the present investigation. The number of individuals ranged from 1 to 23 with a mean intensity of 3.4 parasites per fish. Seasonal incidence and intensity data are presented in Table 14. Examination of these data reveals that infections in adult croakers were fairly consistent throughout the seven month sampling period. The incidence of infection in croakers less than 200 mm in length was found to be 42.2%.

Class Cestoda  
Order Trypanorhyncha  
Suborder Cystidea  
Family Pterobothriidae

A cystic pleurocercus identified as Pterobothrium sp. was recovered from the mesentery and alimentary tract walls of the Atlantic croaker in the present investigation. Species of the genus Pterobothrium have been previously reported as larvae in teleosts and as mature adults in selected elasmobranchs. This metacestode was recovered from 282 of 502 (46.1%) croakers with the intensity of infection recorded under the general categories of light (1-5), moderate (6-10), and heavy (>10) worms per fish. The heaviest infection was 19 worms in a 257 mm female croaker captured in July, 1978. The overall ratio of the number of worms per length of host is shown in Table 15. A total of 120 individuals were reported with a light infection, 75 with a moderate, and 87 with a heavy infection. The data in Table 15 demonstrates that fish less than 200 mm in length are virtually uninfected by Pterobothrium sp. In comparison, larger fish display a greater incidence of infection which in many cases consists of trypanorhynch cysts that display some degree of degeneration and fibrosis. It appears that the prevalence but not

Table 14. Infection incidence and intensity of Lobatostoma ringens

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range
1977												
July					19/31	61.2	3.8	1-9				
Aug.					8/10	80.0	2.8	1-5	3/8	37.5	1.3	1-2
Sept.					4/8	50.0	4.3	1-6	0/6	-	-	-
Oct.					1/1	100.0	1.0	-	16/37	43.2	4.9	1-19
1978												
April	21/50	42.0	2.3	1-7								
May	11/20	55.0	3.5	1-13	6/10	60.0	2.8	1-5				
June					23/50	46.0	2.4	1-7	0/1	-	-	-
July					24/50	48.0	5.9	1-10	0/2	-	-	-
Aug.					31/40	77.5	4.0	1-13	4/19	21.1	1.5	1-2
Sept.	10/30	33.3	3.1	1-11	12/17	70.6	6.4	2-18	42/81	51.9	3.2	1-19
Oct.	25/30	83.3	5.1	1-23	1/1	100.0	-	-				
Total												
In	31/70	45.7	-	-								
Total												
Out	35/60	58.3	-	-								
1977					32/50	64.0	-	-	19/51	37.3	-	-
1978					97/168	57.7	-	-	46/103	44.7	-	-
Cumul.												
Total					129/218	59.2	-	-	65/154	42.2	-	-

Table 15. The occurrence of Pterobothrium sp. in the Atlantic croaker.

Infection Level	Numbers of Fish		Total
	<200 mm	>200 mm	
Light	0	118	120
Medium	1	74	75
Heavy	0	84	87
Total	1	276	277
Total No. of Fish	154	348	502
%	0.6	80.7	56.1

intensity of infection is related to the size of the fish. In other words, more larger fish become infected but not necessarily with a greater number of parasites. Seasonal incidence and intensity data are presented in Table 16. Examination of these data reveals that levels of infection by this metacestode were consistent throughout the 7 month sampling period.

#### Order Tetraphyllidea

Two different tetraphyllidean pleurocercoids were found in the Atlantic croaker in the present investigation. The first, *Tetraphyllidea* sp. A, had four small round ear-like bothridia with an apical sucker. It was recovered from a total of 244 of 502 (49.1%) croakers with an intensity of infection that ranged from 1 to 655 individuals per fish. The seasonal incidence and intensity data presented in Table 17 show that all but one of the croakers harboring this parasite was greater than 200 mm in length. It is evident that the incidence of this metacestode decreases in croakers captured in the latter months of the sampling period.

The second pleurocercoid, *Tetraphyllidea* sp. B, recovered in the present investigation had four leaf-like bothridia with no apical sucker and a body roughly conical in shape. This metacestode was found in only 12 of 502 (2.4%) croakers with an intensity of infection that ranged from 1 to 3 individuals per fish. All specimens of this pleurocercoid were recovered from croakers captured in April at the Chesapeake Bay mouth station.

Table 16. Infection incidence and intensity of Pterobothrium sp.

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range
1977												
July					29/31	93.5	6.4	-				
Aug.					8/10	80.0	10.5	-	1/8	12.5	3.0	-
Sept.					3/8	37.5	10.0	-	0/6	-	-	-
Oct.					1/1	100.0	3.0	-	0/37	-	-	-
1978												
April	46/50	92.0	6.9	-								
May	19/20	95.0	9.3	-	9/10	90.0	8.0	-				
June					42/50	84.0	7.8	-	0/1	-	-	-
July					42/50	84.0	8.0	-	0/2	-	-	-
Aug.					38/40	95.0	6.7	-	0/19	-	-	-
Sept.	18/30	60.0	6.7	-	9/17	90.0	8.6	-	0/81	-	-	-
Oct.	12/30	40.0	7.6	-	0/1	-	-	-				
Total In	65/70	92.9	-	-								
Total Out	30/60	50.0	-	-								
1977					41/50	82.0	-	-	1/51	2.0	-	-
1978					140/168	83.3	-	-	0/103	-	-	-
Cumul. Total					181/218	83.0	-	-	1/154	<1.0	-	-

Table 17. Infection incidence and intensity of Tetracystidea Species "A"

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Mean Inten	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range
1977												
July					13/31	41.9	4.5	2-11				
Aug.					3/10	30.0	2.3	2-3	0/8	-	-	-
Sept.					2/8	25.0	3.5	3-4	0/6	-	-	-
Oct.					0/1	-	-	-	0/37	-	-	-
1978												
April	50/50	100.0	102.0	21-655								
May	20/20	100.0	64.6	3-309	10/10	100.0	27.9	6-73				
June					47/50	94.0	35.5	2-238	0/1	-	-	-
July					33/50	66.0	25.5	1-58	0/2	-	-	-
Aug.					27/40	67.5	16.9	2-102	0/19	-	-	-
Sept.	17/30	56.6	5.1	2-28	4/17	23.5	14.5	2-28	0/81	-	-	-
Oct.	17/30	56.6	13.8	2-85	1/1	100.0	7.0	-				
Total												
In	70/70	100.0	-	-								
Total												
Out	34/60	56.6										
1977					18/50	36.0	-	-	0/51	-	-	-
1978					122/168	72.6	-	-	0/103	-	-	-
Cumul.												
Total					140/218	64.2			0/154	-	-	-

### Order Pseudophyllidea

The remaining cestode recovered from M. undulatus in the present investigation was a segmented pseudophyllidean that displayed two bothria and no differentiation of the genital primordia. Freeman (1973) states that the onset of segmentation in most cases is a valid criterion for the separation of metacestode and adult cestode stages. This is not the case in the present study because of the absence of gonadal maturation. These pseudophyllideans were not considered adults and the Atlantic croaker is not believed to be the final host. A total of 7 of 502 (1.4%) M. undulatus were found to harbor this cestode with an intensity of infection that ranged from 1 to 7 individuals. All infected fish were captured either during April, 1978 at the Chesapeake Bay mouth station or during June, 1978 in the York River.

Phylum Acanthocephala  
Class Acanthocephala  
Order Echinorhynchidea  
Family Rhadinorhynchidae

Dollfusentis chandleri Golvan, 1969 is an acanthocephalan that has been reported from a variety of fish hosts that range from the northern Gulf of Mexico to the coastal waters of New England (Yamaguti, 1963b). This acanthocephalan has been previously reported from the Chesapeake Bay in M. undulatus by O'Rourke (1949) and Huizinga and Haley (1962).

Dollfusentis chandleri was found in the rectum of 330 of 502 M. undulatus collected in the present investigation. The intensity of infection varied from 1 to 153 acanthocephalans with a mean greater than 8 parasites per fish. Seasonal incidence and intensity data of this parasite are presented in Table 18. Incoming croakers possessed a considerably lower incidence of infection than those fish captured at the



Table 18. Infection incidence and intensity of *Dollfusentis chandleri*

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range
1977												
July					26/31	86.6	11.1	1-153				
Aug.					7/10	70.0	6.0	1-9	7/8	87.5	4.9	2-11
Sept.					6/8	75.0	4.3	1-6	3/6	50.0	4.4	1-11
Oct.					1/1	100.0	4.0	-	31/37	83.7	7.1	1-23
1978												
April	1/50	2.0	1.0	-								
May	12/20	60.0	2.6	1-8	3/10	30.0	1.3	1-2				
June					30/50	60.0	2.9	1-11	1/1	100.0	1.0	-
July					36/50	72.0	6.0	1-59	1/2	50.0	41.0	-
Aug.					30/40	75.0	10.3	1-26	15/19	78.9	3.4	1-14
Sept.	15/30	50.0	5.4	1-21	12/17	70.6	8.7	1-24	72/81	88.9	9.0	1-29
Oct.	21/30	70.0	5.6	1-55	1/1	100.0	4.0	-				
Total												
In	13/70	18.6	-	-								
Total												
Out	36/60	60.0	-	-								
1977					40/50	80.0	-	-	41/51	80.4	-	-
1978					112/168	66.7	-	-	89/103	86.4	-	-
Cumul.												
Total					152/218	69.7	-	-	130.154	84.4	-	-

river stations and the bay mouth in the fall. Croakers less than 200 mm in length had a 83.1% level of incidence and an average intensity of 7.7 acanthocephalans per fish. It should be noted that most of these fish represent young of the year which have never migrated out of the estuarine system. The data also indicate that D. chandleri occurs quite often as the only parasite in the alimentary tract of the young fish (Table 19).

The effect of the presence of large numbers of this acanthocephalan on the physical condition of an individual croaker was determined through the computation of a condition coefficient. This coefficient is based on the hypothesis that a large parasite burden will stress a host and cause weight or growth reduction. Only croakers <200 mm were used in this comparison. K-values for infected and uninfected croakers are presented in Table 20. No conclusive difference in condition was evident between the two groups of fish due to the small sample size of uninfected croakers and the comparative size limitations required by the coefficient. Only the coefficients of fish within 10 mm in size could be utilized in a comparison.

Serrasentis socialis (Leidy, 1851) is a member of the family Rhadinorhynchidae which has been previously reported from M. undulatus in Beaufort, N.C. by Linton (1905). This acanthocephalan, unlike D. chandleri, has been reported to infect the Atlantic croaker only as a cystacanth and not as an adult. This larval form has been found in the visceral mesenteries of a variety of piscine intermediate hosts. Adult S. socialis have been reported only from two species of

Table 19. The incidence of *Dollfusentis chandleri* in croakers less than 200 mm.

Date	Total No. Fish <200 mm	Total No, Infected Fish	Fish Infected only w/D.c.
1977			
August	8	7	4
September	6	3	2
October	37	31	11
1978			
April	-	-	-
May	-	-	-
June	-	-	-
July	1	1	0
August	2	1	1
September	19	15	5
October	81	72	23
Total	154	130 (84.4%)	46 (35.4%)

Table 20. K-values for parasitised and non-parasitised Atlantic croakers.

Uninfected Atlantic Croakers <200 mm

	No. Fish Collected	No. Fish Uninfected	K Value	Size Range (mm)
1977				
August	8	1	1.06	158
September	6	2	1.25	183-190
October	37	7	1.14	113-190
Total	51	10	1.15	
1978				
June	1	0	-	
July	2	1	1.03	92
August	19	4	1.03	124-150
September	81	12	1.12	87-170
Total	103	17	1.09	
Cumul. Total	154	27	1.11	

Infected Atlantic Croakers >200 mm

	No. Fish Collected	No. Fish Uninfected	K Value	Size Range (mm)
1977				
August	8	7	1.01	167-193
September	6	4	1.10	191-196
October	37	30	1.06	80-191
Total	51	41	1.05	
1978				
June	1	1	1.12	179
July	2	1	1.20	180
August	19	15	0.91	119-160
September	81	69	1.18	73-198
Total	103	86	1.13	
Cumul. Total	154	127	1.09	

Rachycentron (cobia) in the coastal waters off North America, North Africa, and Australia.

Serrasentis socialis was found in the mesentery of 30 of 502 (5.8%) M. undulatus examined in the present investigation. The number of cystacanths ranged from 1 to 3 with a mean intensity of only 1.4 acanthocephalans per fish. A seasonal decreasing trend of incidence appeared to be present in the data listed in Table 21. Notably, this parasite is absent from young of the year fish.

Phylum Aschelminthes  
Class Nematoda  
Order Ascaridoidea  
Family Anisakidae

The genus Thynnascaris Dollfus, 1933 contains numerous species, reported from piscine definitive hosts, that were described in past literature under the genus Contracaecum. One species, Thynnascaris reliquens was reported from M. undulatus captured in the Gulf of Mexico but it rarely occurred as an egg-producing adult (Norris and Overstreet, 1975). These investigators suggested that the Sheepshead Archosargus probatocephalus, is the normal definitive host for this parasite.

Immature specimens of an unidentified species of Thynnascaris were found lodged in the visceral mesentery of 97 of 502 croakers in the present investigation. The number of individuals ranged from 1 to 4 with a mean intensity of 1.6 parasites per fish. The monthly incidence data presented in Table 22 demonstrates a reduced prevalence of this parasite in fish migrating out of the bay and almost complete absence in croakers less than 200 mm in length.

Table 21. Infection incidence and intensity of Serrasentis socialis

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Inten. Range	Mean	Infect/ Total No.	Incid. (%)	Inten. Range	Mean	Infect/ Total No.	Incid. (%)	Inten. Range	Mean
1977												
July					3/31	9.7	1-3	1.7				
Aug.					0/10	-	-	-	0/8	-	-	-
Sept.					0/8	-	-	-	0/6	-	-	-
Oct.					0/1	-	-	-	0/37	-	-	-
1978												
April	12/50	24.0	1-3	1.6								
May	5/20	25.0	-	1.0	1/10	10.0	-	1.0				
June					5/50	10.0	1-3	1.4	0/1	-	-	-
July					1/50	2.0	-	1.0	0/2	-	-	-
Aug.					1/40	2.5	-	1.0	0/19	-	-	-
Sept.	1/30	3.3	-	1.0	0/17	-	-	-	0/81	-	-	-
Oct.	1/30	3.3	-	1.0	0/1	-	-	-				
Total												
In	17/70	24.3	-	-								
Total												
Out	2/60	3.3	-	-								
1977					3/50	6.0	-	-	0/51	-	-	-
1978					8/168	4.8	-	-	0/103	-	-	-
Cumul.												
Total					8/218	5.1	-	-	0/154	-	-	-

Table 22. Infection incidence and intensity of Thynnascaris sp.

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range
1977												
July					17/31	54.8	2.4	1-5				
Aug.					2/10	20.0	2.0	-	0/8	-	-	-
Sept.					1/8	12.5	1.0	-	0/6	-	-	-
Oct.					0/1	-	-	-	0/37	-	-	-
1978												
April	23/50	46.0	2.1	1-4								
May	4/20	20.0	2.5	2-4	3/10	30.0	2.0	1-3				
June					17/50	34.0	1.9	1-3	0/1	-	-	-
July					13/50	26.0	2.3	1-3	0/2	-	-	-
Aug.					9/40	22.5	1.9	1-3	0/19	-	-	-
Sept.	2/30	6.7	1.0	-	0/17	-	-	-	0/81	-	-	-
Oct.	3/30	10.0	1.0	-	1/1	100.0	1.0	-				
Total												
In	27/70	38.5	-	-								
Total												
Out	5/60	8.3	-	-								
1977					20/50	38.0	-	-	0/51	-	-	-
1978					43/168	25.6	-	-	0/103	-	-	-
Cumul.												
Total					63/218	28.9			0/154	-	-	-

The genus Goezia Feder, 1800, also of the family Anisakidae, has been shown to contain nine separate species reported from piscine hosts (Yamaguti, 1961). None of these species have been previously reported from the Atlantic croaker, thus, the occurrence of an unidentified species of this genus in the present investigation signifies a new host record.

Mature specimens of Goezia sp. were recovered from the 4 of 502 (<1.0%) M. undulatus in the present investigation. Each host was infected by only one nematode which in all cases was recovered from the intestine. All infected fish were mature adults collected in June and September, 1978 in the York River and at the Chesapeake Bay mouth in September, 1978. The low incidence of infection prevented any conclusions from being made on the seasonal distribution of the parasite.

A large number of small unidentifiable larval nematodes were recovered from the intestine of 240 of 502 (47.8%) M. undulatus examined during the present study. The number of individuals ranged from 1 to 46 with a mean intensity of 9.3 parasites per fish. Little credence could be placed on the seasonal trends in data presented in Table 23 because of the counting errors associated with these nematodes. The search for these nematodes was often difficult due to small size and concealment among food items in the gut.

Phylum Annelida  
Class Hirudinea  
Order Rhynchobdellida  
Family Piscicolidae

Calliobdella vivida (Verrill, 1872) is an estuarine leech with a reported distribution that extends along the Atlantic and Gulf coasts



Table 23. Infection incidence and intensity of Nematoda (immature)

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range
1977												
July					5/31	16.1	1.8	1-2				
Aug.					5/10	50.0	3.2	1-8	1/8	12.5	3.0	-
Sept.					1/8	12.5	2.0	-	1/6	16.7	2.0	-
Oct.					1/1	100.0	2.0	-	7/37	18.9	1.9	1-3
1978												
April	29/50	58.0	9.2	3-20								
May	19/20	95.0	15.8	4-42	8/10	80.0	9.0	2-24				
June					42/50	86.0	16.1	1-44	0/1	-	-	-
July					44/50	88.0	11.5	2-46	0/2	-	-	-
Aug.					21/40	52.5	8.1	2-22	7/19	36.8	1.6	1-2
Sept.	8/30	26.7	4.6	3-12	5/17	30.0	4.0	2-6	24/81	27.3	3.0	1-11
Oct.	12/30	40.0	3.5	1-7	1/1	100.0	11.0	-				
Total												
In	48/70	68.6	-	-								
Total												
Out	20/60	33.4	-	-								
1977					12/60	24.0	-	-	9/51	17.6	-	-
1978					122/168	72.6	-	-	31/103	30.1	-	-
Cumul.												
Total					134/218	61.5	-	-	40/154	26.3	-	-

from Massachusetts to Louisiana. Sawyer et al., (1975) listed occurrences of this leech on a variety of piscine hosts that included M. undulatus captured in the coastal waters of Mississippi. This leech infected 7 of 502 (1.4%) Atlantic croakers in the present investigation. Each host was infected by only one leech which in all cases was attached to the external body surface. Calliobdella vivida exhibited a definite seasonal pattern of occurrence in the present investigation. Adult leeches were recovered from croakers captured at the Chesapeake Bay mouth station in the spring and from fish in the York River until June, 1978. Leeches were not seen on fish again during the sampling period until September and October at the Chesapeake Bay mouth station. Leeches recovered from this station were juveniles believed to have recently hatched.

Phylum Arthropoda  
Class Crustacea  
Subclass Copepoda  
Order Cyclopoidea  
Family Ergasilidae

The genus Ergasilus Nordmann, 1932 is a highly successful group of parasitic copepods that are found on both freshwater and marine teleosts throughout the world. Ergasilus labracis, Kroyer 1863 has been previously reported from only one host, the striped bass, Morone saxatilis. Paperna and Zwerner (1976) reported this copepod from striped bass in the Chesapeake Bay. The occurrence of E. labracis on M. undulatus is a new host record.

Ergasilus labracis was found on the gills of 11 of 502 (2.2%) Atlantic croakers collected during the present investigation. The number of individuals ranged from 1 to 500 with a mean intensity of 61.7

copepods per fish. This mean value is not realistic for all infected individuals because of the extremely high number of copepods recorded from one fish. Seasonal incidence and intensity data are presented in Table 24. Notably, this copepod was found throughout the sampling period on adult and young of the year fish captured in both euhaline and mesohaline locations.

Order Lerneopodidea  
Family Lerneopodidae

Clavella inversa Wilson, 1913 has been previously reported from five separate piscine hosts which range from Jamaica and the Dry Tortugas to the Gulf of St. Lawrence. Pearse (1947) reported the occurrence of this copepod on a single M. undulatus taken in Beaufort, N.C.

Clavella inversa was found to infect only 2 of 502 Atlantic croakers in the present study. Each fish was parasitised by only one individual which in both cases was attached to the brachial basket. This copepod was recovered only from incoming migratory croakers in April, 1978. The low incidence prevented any conclusions from being made on the seasonal distribution of this copepod.

Subclass Branchiura  
Order Argulidea  
Family Argulidae

The subclass Branchiura is a small group of crustacea containing six genera that are worldwide in distribution. Argulus is the largest and only branchiuran genus reported from U.S. coastal waters (Cressey, 1972). Argulus bicolor is one of two Argulus species that has been previously reported from M. undulatus. This ectoparasite has been

Table 24. Infection incidence and intensity of Ergasilus labracis

Date	Chesapeake Bay (>200 mm)				York River (>200 mm)				York River (<200 mm)			
	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range	Infect/ Total No.	Incid. (%)	Mean Inten.	Range
1977												
July					0/31							
Aug.					0/10				0/8			
Sept.					0/8				0/6			
Oct.					0/1				1/37			
1978												
April	0/50											
May	5/20	25.0	21.6	1-54	0/10							
June					2/50	4.0	2.0	1-3	0/1			
July					0/50				0/2			
Aug.					2/40	5.0	1.0	-	0/19			
Sept.	0/30				0/17				1/81	1.1	1.0	-
Oct.	1/30	3.3	500	-	0/1							
Total												
In	5/70	7.1										
Total												
Out	1/60	1.7										
1977					0/50				1/51	2.0		
1978					5/168	2.4			1/103	1.1		
Cumul.												
Total					5/218	1.8			2/154	1.3		

recovered from the branchial cavity and body surface of hosts taken from the coastal waters of Virginia to Louisiana.

Argulus bicolor was recovered from the branchial cavity of 2 of 502 Atlantic croakers examined during the present investigation. Only two specimens of this branchiuran were recovered from the infected fish captured in the York River during September, 1978. The low incidence prevented any conclusions from being made on the seasonal distribution of this ectoparasite.

Subclass Isopoda  
Order Cymothoidea  
Family Cymothoidae

Lironeca ovalis (Say, 1818) has been previously reported from M. undulatus and found to range on this host and others in U.S. coastal waters from Massachusetts south into the Gulf of Mexico (Richardson, 1905). This isopod was recovered from the branchial cavity in only 3 of 502 (<1.0%) M. undulatus. It was generally quite large in size but was never recovered in numbers exceeding one individual per fish. All infected fish were mature adults collected in June and July, 1978. This low incidence of infection prevented any conclusions from being made on the seasonal distribution of this parasite.

Pathological Conditions

It was apparent that there was almost a complete absence of pathological conditions in the croakers examined in the present investigation. It was believed that this absence was partially due to the bias induced by the method of sampling. Fish samples obtained from local fisherman were carefully selected to contain fresh healthy looking fish. It can be assumed that fish with pathological conditions would be the first to

die from the stress of being caught in a pound net. Thus, these fish were probably not selected when collections of fish were taken. A single case of lordosis was observed in a 382 mm female croaker captured at the mouth of the Chesapeake Bay in October, 1978. The data on the parasites recovered from this fish indicate that this condition had no detrimental or other effects on the ability of this host to feed. This conclusion was supported by the presence of food in the gut and the absence of large numbers of different parasites. The aetiological agent responsible for this condition are unknown.

#### Statistics and the Comparison of Parasite Communities

Statistical tests were employed to better understand the prevalence and intensity of parasitism, to elucidate the ecological relationships of association, and the concepts of diversity, dominance and similarity of parasite faunas recovered from different geographical areas, seasons, and sizes of hosts.

Association between the seven most prevalent intestinal helminths (greater than 20% incidence) was expressed as Cole's coefficient and analyzed in terms of frequency of occurrence and levels of infection. Table 25 presents the Cole's coefficient for all possible pairs of the helminths and the Chi-square values testing observed vs. expected values for frequency of occurrence. In general, a value of Cole's coefficient larger than 0.7 (regardless of the sign) is considered to be significant. Only one pairing (L. setiferoides and O. vitellus) demonstrated a significant Cole's coefficient and that was a negative association. Negative associations were represented by 12 pairs while positive associations composed the remaining 9 helminth pairs. Signi-

Table 25. Cole's coefficient and Chi-square values for the frequency of occurrence of helminth pairs taken from croakers.

Helminth Pairs		$C_{AB}$	Total Chi-square Values
L. setiferoides	& O. fimbriatus	-0.16	1.20
"	& O. vitellosus	-0.67	4.23*
"	& S. tenue	0.01	3.69
"	& D. leiostomi	0.14	5.60*
"	& D. chandleri	0.07	0.49
"	& L. ringens	-0.07	0.87
O. fimbriatus	& O. vitellosus	0.35	8.48*
"	& S. tenue	-0.28	2.35
"	& D. leiostomi	-0.05	0.28
"	& D. chandleri	-0.12	2.28
"	& L. ringens	-0.09	1.09
O. vitellosus	& S. tenue	0.56	3.05
"	& D. leiostomi	-0.29	0.99
"	& D. chandleri	-0.42	3.81
"	& L. ringens	-0.02	0.01
S. tenue	& D. leiostomi	0.09	0.87
"	& D. chandleri	0.10	1.71
"	& L. ringens	-0.12	1.70
D. leiostomi	& D. chandleri	0.06	0.82
"	& L. ringens	0.11	1.83
D. chandleri	& L. ringens	0.04	0.45

\*Significance at .05 level.

ficant Chi-square values indicating an observed frequency of occurrence different from the expected values was found in 3 of the 21 pairings of parasites. Opecoeloides vitellosus displayed an incidence level less than 20% but was included in the analysis due to the occurrence of two species in this genus with each occupying a distinct region of the gut.

Association between helminth pairs was also examined in the terms of levels of infection. A reduction in parasite numbers or complete elimination from the host are two results of interference competition. The Mann-Whitney U test and the Wilcoxon two sample test both conclusively demonstrated that the majority of helminths did not have a significant change in numbers when in the presence or absence of the other member of the pair. A significant level of infection occurred in only one of 42 pairings. A lower level of infection for O. fimbriatus was apparently associated with the presence of D. leiostomi.

The structure of the parasite community or parasitocoenosis can be described by the indices of diversity and dominance, but must be interpreted in conjunction with the raw count data. Table 26 presents a summary of the data with community diversity, individual diversity, and redundancy in a monthly sampling format. It is apparent from the data that extensive explanations are necessary to describe the change in the parasitocoenosis on a monthly basis but not when concerned with gradual trends of each category in the table. The number of species ranged from 9 to 21, with the maximum number present in the June York River sample and the minimum found in the young of the year fish. The size of the community (expressed as mean no. parasites/fish) was greatest in the fish migrating into the Bay in the spring with a rapid decrease



Table 26. Community diversity, individual diversity and redundancy values for parasite communities of the croaker in monthly samples.

Sampling Location/Date	No. Species	Mean No. Parasites/Fish	Community Diversity(d)	Individual Diversity( $\bar{d}$ )	Redundance
Ches. Bay	April	16	123.10	136.64	1.11
	May	15	93.32	163.25	1.76
	May	14	57.09	139.61	2.45
	June	21	73.18	184.00	2.52
York (1978)	July	15	50.42	135.51	2.71
	August	15	42.07	125.07	2.98
	Sept.	14	49.21	110.95	2.26
	Oct.	-	-	-	-
Ches. Bay	Sept.	15	23.11	68.85	2.99
	Oct.	15	65.10	195.72	3.01
	Oct.	15	65.10	195.72	3.01
York (1977)	July	13	31.13	77.60	2.50
	August	10	25.33	60.89	2.44
	Sept.	11	19.21	51.00	2.68
	Oct.	0	0	0	-
<200 mm	1977	9	10.82	17.01	1.57
	1978	9	13.05	22.05	1.69
					>1.00
					>1.00

and leveling off until the October sample at the Chesapeake Bay mouth. The young of the year fish also displayed the smallest community size totals. Community diversity, which is an expression of both equitability and community size, was at a high peak in the June (York River) and October (Chesapeake Bay) samples. The low value was again seen in the smaller fish. Individual diversity or species richness gradually increased throughout the 1978 sampling season (with exception of September) and was in all cases inversely proportional to the redundancy values. The greatest dominance was seen in the April sample and in the young of the year fish.

Similarity of parasite faunas among the monthly samples in the York River and those taken at the Chesapeake Bay station were compared utilizing two separate analytical methods. A qualitative comparison was determined through the computation of Sorenson's index for two parasite categories: all parasites and Digenea only. The indices were arranged in a trellis diagram and are presented in Table 27. A decrease in similarity was evident for the Digenea when spring migratory croakers (Chesapeake Bay in) were compared to those fish captured later in the season. The most dissimilar groups were the parasites recovered from fish entering the Bay in the spring (Chesapeake Bay in) and those migrating out of the Bay in the fall (Chesapeake Bay out).

The second method used to determine the similarity of parasite faunas in different size fish from separate geographical areas was numerical classification or cluster analysis. The noraml classification of this cluster analysis shown in Figure 2 expresses the overall "likeness" or "similarity" among assemblages of organisms. The station

Table 27. Sorenson's index of similarity for samples of croakers by time of sampling and size of fish.

	Ches. Bay In	May	June	July	August	September	October	Ches. Bay Out	Croakers Less than 200 mm TL
Ches. Bay In		78.8	80.0	70.5	76.5	60.6	53.8	76.5	55.1
May	72.7		80.0	89.7	89.7	78.6	66.7	89.7	66.7
June	71.4	76.9		83.3	83.3	74.2	50.0	88.9	51.6
July	66.7	90.9	85.7		93.3	75.9	54.5	86.7	64.0
August	66.7	90.9	85.7	100.0		75.9	54.5	93.3	64.0
September	54.5	80.0	76.9	90.9	90.9		57.1	82.8	66.7
October	50.0	57.1	40.0	50.0	50.0	57.1		54.5	35.3
Ches. Bay Out	54.5	80.0	76.9	90.9	90.9	80.0	28.5		64.0
Croakers Less than 200 mm TL	44.4	75.0	54.5	66.7	66.7	75.0	40.0	75.0	

Right side of trellis = all parasites recovered from croakers in 1978.

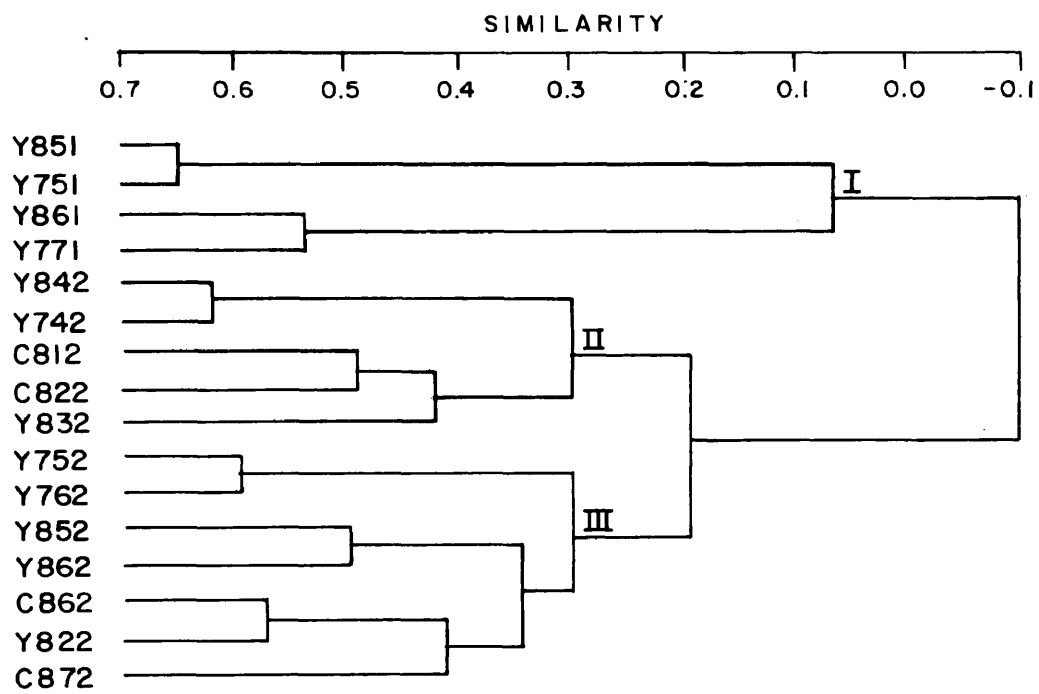
Left side of trellis = all Digenea recovered from croakers in 1978.

Ches. Bay IN = April & May 1978

Ches. Bay OUT = September & October 1978

All other months are from the York River in 1978

Figure 2. Normal classification hierarchies resulting from the agglomeration of collections of Atlantic croaker parasites.  
(Collection groups for nodal analysis indicated by Roman numerals.)



codes used on the classification hierarchy can be interpreted via the following key: 1st column = location, Y = York River, C = Chesapeake Bay; 2nd column = year, 7 = 1977, 8 = 1978; 3rd column = month, 1 through 7 corresponds with months April through October; 4th column = host size, 1 = <200 mm, 2 = >200 mm. The inverse cluster presented in Figure 3 reflects the similarity in distribution patterns among species. The Canberra-metric resemblance measure in conjunction with the flexible sorting strategy resulted in a bias toward small groups joining to form separate branches of the hierarchy. The variable stopping rule used to determine "reasonable" groups of entities resulted in 3 stations and 6 parasite groups.

Normal classification clearly separated stations according to the criteria of size of fish and month of sampling (Figure 2, Table 28). Parasites recovered from croakers less than 200 mm (Group I) were apparently quite different from those found in larger fish. The demarcation between the parasite fauna in larger fish seems to occur between the months of July and August. Stations in Group II consist of fish taken April through July while Group III are the fish taken August through October with the exception of Station Y822. This station is composed of 10 fish sampled during May from the York River and is believed to represent a misclassification.

The inverse classification separated parasite species into six groups (Figure 3, Table 28) based on similarity of distribution patterns. These patterns are difficult to explain because very little is known about the life cycles of most of the parasites. The ecological concepts utilized in nodal analysis aid in this explanation through the

Figure 3. Inverse classification hierarchies resulting from agglomeration of collections of Atlantic croaker parasites. (Species groups for nodal analysis indicated by Roman numerals.)

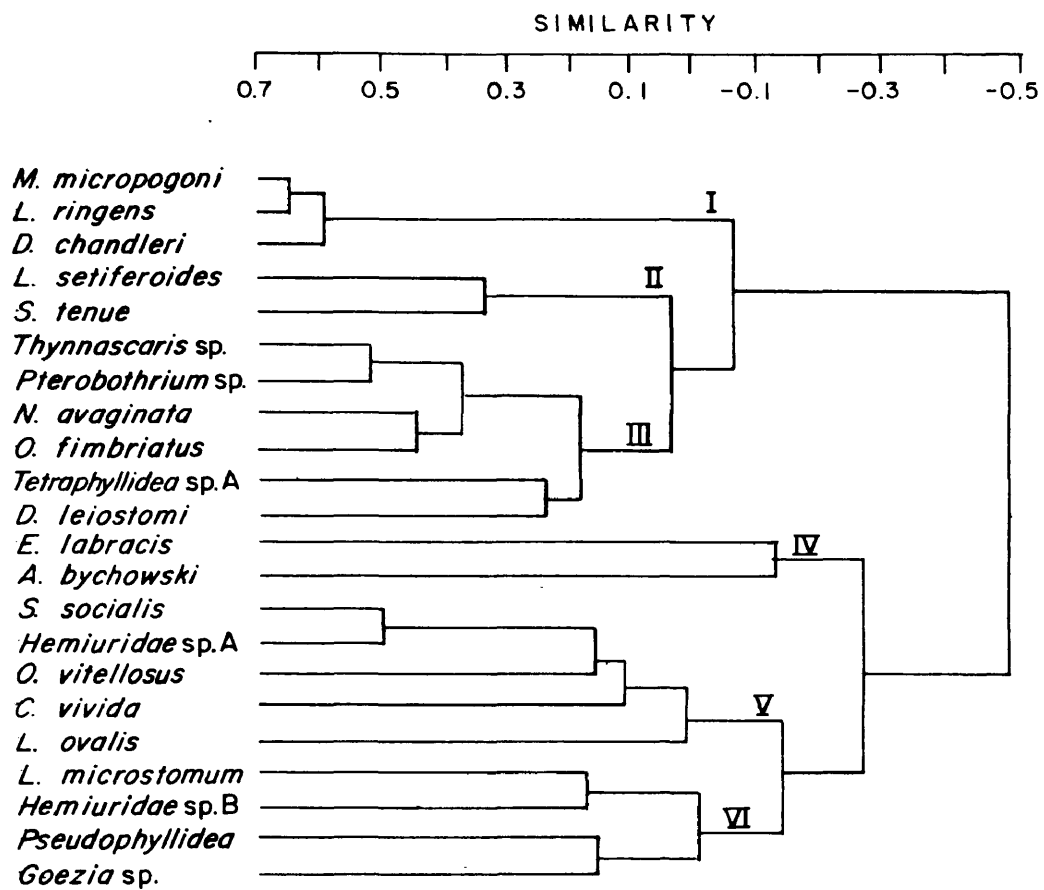




Table 28, Nodal Analysis Groups

Collection Groups	Species Groups
I. Y851 Y751 Y861 Y771	I. <u>M. micropogoni</u> <u>L. ringens</u> <u>D. chandleri</u>
II. Y842 Y742 C812 C822 Y832	II. <u>L. setiferoides</u> <u>S. tenue</u>
III. Y752 Y762 Y852 Y862 C862 Y822 C872	III. <u>Thynnascaris</u> sp. <u>Pterobothrium</u> sp. <u>N. avaginata</u> <u>O. fimbriatus</u> Tetraphyllidea sp. A <u>D. leiostomi</u>
	IV. <u>E. labracis</u> <u>A. bychowski</u>
	V. <u>S. socialis</u> Hemiuridae sp. A <u>O. vitellosus</u> <u>C. vivida</u> <u>L. ovalis</u>
	VI. <u>L. microstomum</u> Hemiuridae sp. B Pseudophyllidea <u>Goezia</u> sp.

interpretation of the following tables: constancy (Table 29), fidelity (Tables 30, 31) and abundance (Table 32). These tables indicate shifts in species occurrence and abundance which are responsible for the differences in station groups. The incidence of parasites in species Group I is constant for both the size of fish and season of sampling. Constancy and fidelity values are at a maximum in all three collection groups while the abundance appeared to increase in larger fish taken in the sampling period and to be considerably less in the younger and smaller fish. Species Group II consisted of two digenes which were present in juveniles and showed an increase in fidelity, constancy, and abundance in the stations sampled later in the season. Parasites in Group III appear to be ubiquitous. These parasites are found in juveniles but demonstrate little seasonality of incidence in other station groups. It does appear though that these parasites are more abundant in the early sampling months (collection Group II) than in the later months (collection Group III). Species in Group IV are unique because of their high fidelity value for the smaller croakers of collection Group I. In contrast, parasites in Group V do not occur in the smaller fish. These parasites show a definite occurrence and abundance which decreases in the stations of the latter part of the sampling period. The remaining group of parasites (VI) are also absent in juveniles but display a greater abundance and large constancy and fidelity values for croakers taken in the early part of the summer (station Group II).

Table 29. Constancy Matrix

		Collection Groups		
		1	2	3
Species Groups	1	1.000	1.000	1.000
	2	0.500	0.500	0.786
	3	0.583	1.000	0.952
	4	0.500	0.200	0.143
	5	0.000	0.840	0.343
	6	0.000	0.350	0.036

Table 30. Cell Fidelity Matrix

		Collection Groups		
		1	2	3
Species Groups	1	1.000	1.000	1.000
	2	0.800	0.800	1.257
	3	0.667	1.143	1.088
	4	2.000	0.800	0.571
	5	0.000	2.036	0.831
	6	0.000	2.800	0.286

Table 31. Cell Fidelity Chi-square Matrix

		Collection Groups		
		1	2	3
Species Groups	1	0.271	0.267	0.262
	2	0.133	0.240	0.933
	3	16.095	3.219	1.646
	4	1.500	0.000	0.381
	5	12.392	17.130	0.443
	6	1.286	7.314	1.306

Table 32. Abundance Matrix

		Collection Groups		
		1	2	3
Species Groups	1	1.001	1.259	0.814
	2	0.082	1.029	1.504
	3	0.057	2.233	0.658
	4	2.010	0.290	0.930
	5	0.000	2.696	0.360
	6	0.000	2.933	0.190

## DISCUSSION

The composition of a parasite community is dependent upon the biotic and abiotic characteristics of the habitats of the fish as well as the physiological and morphological features of the parasite and host (Margolis, 1965). The first set of factors determines the opportunities for contact between parasite and host while the latter set includes the adaptations that permit the parasite to remain associated with the host and continue its development. It can be concluded then that in addition to the influence of the changing environment resulting from migration that the biology of the croaker plays an important role in the composition of the parasitocoenose.

### Biology of the Atlantic Croaker

Previous life history studies of M. undulatus by Hildebrand and Cable (1930) and Wallace (1940) indicate that mature adult croakers enter the Chesapeake Bay with the onset of warmer spring temperatures and leave as early as August to spawn offshore. This southerly oceanward migration has been shown by Pearson (1932) and Haven (1954) to range as far south as the coastal waters of North Carolina. Thus, each year adult croakers can be found living and feeding in both estuarine and offshore habitats. In contrast, the majority of the young of the year fish enter the estuaries in the late fall, winter over, and remain until late summer of the following year. Due to the prolonged spawning period, it has been shown by Chao and Musick (1977) that young of the year croaker spawned in the spring may enter the bay in

May and leave in the fall of the same year. Chao and Musick (1977) postulated that size is the determining factor for offshore migration. It was found by these investigators that very few young of the year croakers greater than 130 mm TL stayed in the York River during the winter.

It was established by Polyanski (1958) that the parasite fauna of migratory fishes, similar to the Atlantic croaker, are directly influenced by changing diet, habitat, and physical conditions. In particular, the diet of fish can be a function of size as well as the movement into different habitats. The sampling regime of the present study does not allow the analysis of stomach contents and parasites taken from fish captured directly from an offshore habitat but it does permit the examination of fish of different size migrating between the ocean and the Chesapeake Bay.

There have been numerous food habit studies conducted on the Atlantic croaker along the Atlantic seaboard and the Gulf of Mexico. A total of fifteen investigations in the latter location have been summarized by Overstreet and Heard (1978). A list of the reports from the Atlantic coast is presented by Chao and Musick (1977). The majority of the studies from this area appear to consist of only generalized listings with no consideration of age, seasonality, and sampling location. The most pertinent studies geographically are the investigation by Roelofs (1954) in North Carolina coastal waters and the food habit study on juvenile croakers by Chao and Musick (1977) in the Chesapeake Bay. Roelofs (1954) reported that the food items examined from 159 adult croakers consisted of only 9 separate taxa.



In contrast, Overstreet and Heard (1978) reported 83 taxa from croakers captured in the Gulf of Mexico while Stickney et al. (1975) listed 58 taxa as food items in croakers sampled in Georgia. These reports demonstrate that fish from different geographical areas do not always feed on the same items or in the same proportions. Overstreet & Heard (1978) state that those factors which govern composition of a diet are still not well studied and most are unknown.

The Atlantic croaker possesses adaptations necessary for feeding on and in the substratum (Chao & Musick, 1977). Stickney et al. (1975) have suggested that the croaker may be opportunistic in its food habits. Darnell (1958) and Overstreet & Heard (1978) provide evidence of learning behavior and feeding specialization in the Atlantic croaker. Specific individuals from a collection of confined fish had exclusively fed on specific food items different from their counterparts. In general, these investigators found that most croakers fed on a variety of items. The data from the present study reveals that a tendency to specialize on a particular food item exists within size groups of croakers. The Chi-square test with separate 2X2 contingency tables indicates that a significant difference in frequency of five food items exists between croakers less than or greater than 200 mm TL. It was also shown that these five groupings of food items make up a large part of the croaker diet. The prey organisms of M. undulatus increase in size with the increasing size of the predator. This is evident in the increased consumption of crabs and fishes by croakers of larger sizes. The studies by Hanson (1969) and Overstreet & Heard (1978) both demonstrated that total length has an influence on the food items consumed by the croaker. The low incidence of penaeids and the importance of

mysids in the diet of these fish is in agreement with data from the coastal waters of North Carolina (Roelofs, 1954) and Georgia (Stickney et al., 1975). The absence of penaeids in the diet of croakers of these areas has been postulated by Stickney et al. (1975) to be due to the behavioral activities of these shrimp or the possible greater abundance of mysids.

Some of the gut contents in the Atlantic croaker appear incidental and may not be of any nutritional value to the fish. The present investigation, like several past studies, found that detritus and sediment make up a portion of the gut contents. Stickney and Shumway (1974) reported that M. undulatus does not exhibit cellulase activity in the gut. Therefore, the majority of plant detritus is nutritionally useless to the fish. An explanation for the presence of the detritus in the gut is the inferior placement of the mouth which results in the loss of visual contact of the food being eaten. The croaker is therefore prone to ingesting extraneous material.

A review of the scientific literature indicates that a considerable amount of work has been done on the biology of Micropogonias undulatus. Several aspects of life history and population dynamics are still unclear (White & Chittenden, 1977). Many early workers, including Welsh & Breder (1923) and Wallace (1940), attempted to develop reliable scale reading methods for age determination. Joseph (1972) and Suttkus (1955) demonstrated that ageing by the scale method is difficult to apply to the croaker due to its migratory habits and extended spawning season. A validated method for scale reading was established by White and Chittenden (1977) but one researcher still considers this conventional

ageing method only moderately successful to best (Mercias, 1978).

Several other methods of age determination in the Atlantic croaker have been studied because of the problems associated with scale interpretation. These methods include the reading of otoliths, age-length frequency, and eye lens-weight ratios. Westrheim & Ricker (1978) demonstrated that an age-length key in fish with an overlap in lengths between successive ages would produce a distribution with systematic bias. Due to this factor, this ageing method was found completely unsuitable for the Atlantic croaker. Errors in this method could result from the large size-age overlap caused from the prolonged spawning season. Mercias (1978) claimed ageing by otoliths in the croaker was unsatisfactory due to the overall difficulty in working with the brittle otoliths. He preferred an ageing method using the comparative weight of eye lens and he applies this method on to croakers up to age class 2 with accuracy similar to that for standard length frequency analysis.

Reading of croaker scales has been problematical because two marks are formed each year except during the first year in which only one is formed. White & Chittenden (1977) established a methodology which distinguished annuli through criteria which placed heavy emphasis on cutting over and differential spacing of circuli. These same investigators found that no mark was formed during the first winter and quite often some croakers form no marks at all during their first year of life. In this case, the first mark is a warm-period mark and the second more distinct mark is the cold-period mark. Warm-period marks form from approximately May to November and cold-period marks from December to April.

White & Chittenden (1977) state that the standard hatching date for fish in the northern hemisphere is the first of January. This date has biological reality for the northern waters because spawning is restricted in time and growth seasons tend to be short. White & Chittenden found that croakers in the Carolinian province possess a long growing season and spawning can range over two calendar years. They believed that croakers captured north or south of Cape Hatteras can be aged using October 15 as the hatching date. All age determination done in this study was checked through the comparison of marks and the proposed time of formation. All sampling was done during the warm months (April-October) therefore, a complete picture of the time sequence when marks are formed was not possible.

In most cases, the young of the year captured June through October demonstrated no marks on their scales. Those fish which displayed one mark were postulated to have been spawned as early as the late summer. Fish in the 1+ and 2+ age categories displayed cold-period marks close to the scale margin in the early spring. These same age fish taken later in the year showed the formation but not termination of a warm-period mark.

Haven (1954) documented that a fall and winter mark form each year on the scales of fish from the Chesapeake Bay. White & Chittenden (1977) believe that croakers north of Cape Hatteras survive longer than those fish in the Carolinian province thus, these fish often display many marks on their scales. Data in the present investigation agree with the length frequencies for the young of the year croakers taken in the Chesapeake Bay by Haven (1957). Haven reported the size of these

young fish to range from 150-220 mm with a mode of 175 mm while fish collected from June to October in the present study ranged from 73-218 mm with a mean of 148 mm. The growth rate of these croakers in cold temperate waters seems to be quite similar to the fish in warmer waters (Gunter, 1945; Parker, 1971; Gallaway & Strawn, 1974).

Past investigations on the croaker stocks in northern temperate areas have shown no segregation or major life history difference between male and female croakers. It was found in the present investigation that female croakers were generally larger in size than males of the same age. An explanation for this difference appears limited by the small sample size of male croakers, the different sampling times for fish within each age group, and the long spawning season for this fish. Bias from the small sample size and the large variation in the amount of first year growth are postulated to be mainly responsible for the length difference.

The overall growth rate is one of the few life history aspects which is similar between croakers from cold and warm temperate waters. Life history differences exhibited by the croakers in more northern areas include: a spawning season which is thought to begin and end earlier (August-December), the attainment of maturity approximately one year later in time, and a greater typical maximum age (2-4 years) and size (500 mm). This large size has been shown to be important to the commercial food fishery in the northern temperate areas. White & Chittenden (1977) believe that a high mortality results in an overall small size and in the absence of a highly successful commercial fishery based on the Atlantic croaker in the Carolinian province.

Numerous studies demonstrate radical reproductive differences in the croakers taken from the Atlantic coast and those from the Gulf of Mexico. Welsh & Breder (1923) found the northern croaker to mature between their 3rd and 4th years while Pearson (1929) documented that croakers from the coastal waters of Texas spawn at the end of their second year. White & Chittenden (1977) reported that croakers from the Gulf of Mexico mature between 140-180 mm in length. This data reinforces the belief of Chabanand (1929) and Hildebrand & Cable (1930) that individuals of the same species mature at an earlier age in warmer climates.

The present investigation revealed that all fish captured in the spring had gonads which were either immature or in the resting stage (I) of development. A progression of gonadal ripening up to the 4th stage of development was evident from all mature individuals taken in the summer and fall sampling periods. Wallace (1940) stated that males begin their spawning migration before the females. Data from the present study does not indicate that either sex ripens earlier than the other. The smallest size of each mature individual of each sex was found to agree with prior reports (Wallace, 1940; Haven, 1957) from the northern temperate waters.

#### Parasite Taxonomy and Life Cycles

The present study compared the parasite fauna of fish that migrated between two different habitats. It was not possible to sample offshore throughout the winter, therefore it must be assumed that the parasites in croakers entering the Bay in the spring represent mostly offshore species. Changes in the parasite fauna can be attributed to either

direct or indirect effects of environmental conditions, the parasites themselves, or the presence or absence of intermediate hosts that are necessary for the completion of life cycles. The digenetic trematodes appear to best demonstrate the gradient of change between the ocean and estuarine habitats. This may be attributed to their strong dependence on the specific intermediate hosts of their indirect life cycle and the fact that most are short-lived. Thus, it can be concluded that in order to analyze the alteration of the parasitocoenose in a migrating croaker the life cycles of the parasites themselves must be understood.

The distribution of Lepocreadium setiferoides is one of the best examples of the faunal change which occurs in migrating Atlantic croakers. The life cycle of this digene has been well studied and includes intermediate hosts that are found only in an estuarine habitat (Martin, 1938; Stunkard, 1972). The life cycle includes the development of larval stages in the marsh snail, Ilyanassa obsoletus (Say), the encystment of metacercaria in the turbellarian, Procerodes warreni or the annelid, Spio sp., and the development of the adult in a teleost like the summer flounder, Paralichthyes dentatus. Subsequent experimentation by Stunkard (1972) demonstrated that other estuarine organisms could serve as either the secondary intermediate or final host. Digenes are normally quite specific for the first intermediate host therefore it is postulated and reinforced by the data of the present investigation that the hosts involved in the life cycle of L. setiferoides are found in the Chesapeake Bay. The absence of this trematode in all of the croakers migrating into the Bay also provides data for speculation that the life expectancy of adult L. setiferoides in the croaker is less than the five months spent offshore by the fish.

Sogandares-Bernal and Hutton (1960) noted that the status of many species in the genus Lepocreadium was uncertain. Stunkard (1969) found that many specific descriptions were inadequate due to the small number and poor quality of specimens. Edwards & Nahhas (1968) constructed a key to this genus which presented only 24 of 31 described species as valid members of the genus. Two of these species have been reported from the Atlantic croaker. Lepocreadium micropogoni and L. floridanus were reported in the croaker from North Carolina by Pearse (1949) and Diaz and Johnson (1974), respectively.

Lepocreadium micropogoni appeared in the species key for Lepocreadium but it is considered to be species inquirenda by Sogandares-Bernal and Hutton (1960) due to the badly damaged holotype and the weak description. To add to the confusion, L. micropogoni is thought to be a synonym of L. ovale by Stunkard (1969) and either L. trullaforme or L. pyriforme by Overstreet (pers. comm.). Past identifications of these two species has been so poor that both are considered to have had an assemblage of heterogenous species placed under the same name. The species of Lepocreadium recovered in the present study was identified not through the use of a key but by the size of the eggs (Overstreet, pers. comm.). Much more work is needed not only on the species of this area but on all species of Lepocreadium.

Stephanostomum tenue, like L. setiferoides, did not occur in croakers migrating into the bay, but was found in increasing numbers with the progression of the summer. Martin (1939) reported that the life cycle of this digene is estuarine in nature. The production of rediae and cercariae was found to take place in the digestive gland of



the marsh snail, Ilyanassa obsoletus, the development of metacercariae in cysts in the liver of Menidia menidia, and the maturation of this digene in the puffer, Sphaeroides maculatus. Yamaguti (1975) reported that S. tenue matures after approximately two weeks of growth in the final host. The amount of time that this digene remains viable in each life cycle stage is unknown, but juvenile S. tenue was recovered every month sampled in the York River. These data indicate that croakers acquire this parasite through the consumption of intermediate hosts located in the Chesapeake Bay estuarine system. It has been shown that larger croakers include fish as part of their diet but it is not known whether these fish include M. menidia. The absence of S. tenue in fish less than 200 mm TL appears to support the hypothesis that the second intermediate host is a fish. The smaller sized croakers consume less fish, thus can be expected to contain a reduced number of S. tenue.

A total of three Stephanostomum species have been previously described from the Atlantic croaker. Stephanostom dentatum and S. interruptum were reported as mature adults in the alimentary tract of croakers by Linton (1905) and Sparks & Thatcher (1958), respectively. Yamaguti (1958) listed a variety of piscine intermediate hosts (including M. undulatus) in which S. imparspine has been found to occur. The final host of this species is the cobia, Rachycentron canadis.

The complete absence of the three previously mentioned species and the contrasting high incidence of S. tenue was unexpected in this study because this species have never been reported from the Atlantic croaker. Stephanostomum dentatum and S. imparspine have both been reported in the

croaker from the coastal waters of North Carolina but neither occurred in this study. Some ambiguity surrounds the past reports of S. tenue because of the use of old names. Distomum tenue tenuissime, which is considered synonymous with S. tenue, has never been reported from the Atlantic croaker. However, Linton (1905) reported Distomum tenue from M. undulatus in Beaufort, N.C. There is no mention that this species is the same as S. tenue therefore, the present study represents a new host record.

Lecithochirium microstomum is one of many trematodes in the family Hemiuridae which occur as parasites in the stomach of fishes (Schell, 1970). In contrast to the two previous digenes, specimens of L. microstomum were recovered only from large croakers (greater than 200 mm TL) migrating into the bay in the spring. The life cycle of this digene is unknown but postulated to be oceanic in nature due to the sole occurrence of this parasite in early spring samples and past reports in the literature. Yamaguti (1958) reported that this digene has been recovered from ten separate host species. A common factor which appears to be present in the majority of these hosts is that most are predatory on other fish. Therefore, it is postulated that the second intermediate host of L. microstomum may be a fish. The absence of winter oceanic sampling in combination with the low incidence of infection revealed little information to support any further postulation on the life cycle of this digene.

Taxonomic uncertainty exists at the generic level of this group of hemiurids. Looss (1907) distinguished the genera Lecithochirum and Sterrhurus with three characteristic differences which have been notice-

ably weakened by the addition of new species, Jones (1943) stated that the characters used to separate the genera were variable and should be used for no more than a specific value. She did not reduce the two genera to synonymy but did suggest that further work was needed. Crowcroft (1946) attempted to redefine the genera on the presence of a "prostatic vesicle" in Lecithochirium and an "ejaculatory vesicle" in Sterrhurus. There appears to be an inconsistency in the presence of these vesicles, thus identifications were based on the presence of a preacetabular pit. Several authors have considered this structure to be a rather weak characteristic and there is a feeling that the two genera should be synonymized (Overstreet, per. comm.).

Taxonomic problems also exist within Lecithochirium. The species in the present study is considered to be L. microstomum but due to the weak description of the sinus sac by Chandler (1935) it is believed that this species and L. synodi may be the same (Manter, 1947). Differences in these species seem restricted to egg width and the shape of the sinus sac. Even if these two digenes are synonymized, the occurrence in the present investigation is a new host and locality record for L. microstomum.

The other hemiurid species recovered in this study were present in such small numbers and were of such poor quality that definitive taxonomic statements could not be made about either species. "Species A" is a mature digene which was recovered throughout the 1978 sampling period. The only important aspect regarding the occurrence of this unnamed digene is its complete absence in young of the year fish. Careful preparation of additional specimens should yield a positive identification

for this species. In contrast, hemiurid "B" is an immature digene whose occurrence in the croaker may represent the use of this fish as either an intermediate or "dead-end" host. This postulation is derived from the fact that very few specimens were recovered and all were in an immature stage of development. The croaker may serve as an intermediate host because this digene may utilize a predator, that feeds on M. undulatus, as a final host. Most parasites occur in hosts by chance, therefore it is not unreasonable to postulate that the presence of this digene in the croaker is not part of its normal life cycle. This hemiurid may survive in the croaker but it may never mature or may never end up in its normal definitive host. It is postulated that the final host of species "B" is most probably a fish (Overstreet, pers. comm.).

Two taxonomically similar species of the genus Opecoeloides, O. fimbratus and O. vitellosum, were recovered in the present study. In past investigations both species have been known under the name of Distomum vitellosum. Linton (1934) first separated these digenes into separate species of the genus, Cymbephallus. Characteristics used for separation included the number of acetabular papillae, lobulation of the testes, size of ova, and general size of the worm. Uncertainty continued to surround these digenes when vonWicklen (1946) placed C. fimbriatus into the new genus Fimbriatus. The generic character utilized for the separation was the presence of two ani and one uroproct. These characters were later found inadequate by Sogandares-Bernal & Hutton (1959) because Fimbriatus is monotypic and the presence of the determining characteristics is dependent on the amount of contraction undergone by the posterior end of the body. Sogandares-Bernal &

Hutton (1959) considered Fimbriatus a synonym of Opecoeloides due to the great similarity between the digenes and the discreditation of the ani and uroproct characteristic. Separation of these two digenes in the present investigation was dependent upon the presence of minute rodlets in the parenchyma of O. vitellosus (Hopkins, 1941b).

Opecoeloides fimbriatus is the most prevalent of the two opecoelid trematodes recovered in the present investigation. This digene was recovered from Atlantic croakers throughout the 7-month sampling period with little change in either incidence or intensity. Thus, conclusions cannot be made from the data regarding either seasonality or habitat preference. The life cycle of this digene has not been thoroughly investigated or documented for all stages. Sogandares-Bernal & Hutton (1959) report the occurrence of the metacercariae in the penaeid, Penaeus duorarum. Wass et al. (1972) reports that this shrimp is an occasional inhabitat of the Chesapeake Bay and its tributaries. Thus, it is possible that this shrimp may serve as the intermediate host for O. fimbriatus. Yamaguti (1958) lists a total of seven separate piscine hosts in which the adult stage of this digene has been recovered. The majority of these hosts are sciaenids that are reported to feed almost exclusively on the bottom.

Opecoeloides vitellosus occurred in croakers migrating into the bay in the spring and declined slightly in incidence with the progression of the summer. This opecoelid species, unlike O. fimbriatus, was not found in smaller croakers (less than 200 mm in length). This absence in smaller fish and the relatively constant incidence in larger fish appears to indicate that the life cycle of O. vitellosus may be

dependent on intermediate hosts from an oceanic habitat or that the intermediate hosts are large in size. Hunninen & Cable (1941) documented that the life cycle of this digene is estuarine in nature. The first intermediate host was found to be the snail, Mitrella lunata, while the second, intermediate hosts were two amphipods, Ampithoe longimana and Carinogammarus mucronatus. Wass et al. (1972) indicated that these invertebrates are found quite often in the Zostera beds of the Chesapeake Bay.

Based on the known life cycle and the fact that the intermediate hosts are present in the Bay, O. vitellosus should be absent in fish taken early in the year and present in later ones. An explanation for the presence of this trematode in incoming fish seems to be restricted to the unusual fact that all specimens of O. vitellosus were taken from croakers captured in the month of May. It is possible that this trematode was acquired during the month of April when croakers may have been actively migrating in and out of the Bay with the tide. The complete absence of this trematode in smaller croakers seems unusual if it is assumed that the life cycle is actually estuarine in nature. Amphipods constitute a large part of the diet of smaller croakers and it seems reasonable to assume that this trematode would be first acquired by these fish. Further investigation appears necessary to resolve these problems.

Diplomonorchis leiostomi was initially described from the spot, Leiostomus xanthurus, and the pigfish, Orthopristis chrysopterus taken from collections in Beaufort, N.C. (Hopkins, 1941a). Since that time approximately eight other fishes have been described as hosts, including

M. undulatus. Unlike the other digenes recovered in the present study, there are no taxonomic problems or uncertainties associated with the two members of Diplomonorchis. Both species differ significantly from the other members of the family Monorchiidae in shape of the excretory bladder and location of vitellaria.

In the present study, the incidence of D. leiostomi remained essentially constant in seasonal catches of croakers captured in different locations. This digene was also found to infect all age categories of croakers throughout the entire sampling period. The life cycle of D. leiostomi is not known but the high incidence of this digene in young of the year fish indicates that the intermediate host must be present in the Bay and a common food item. The occurrence of this digene in older fish during all months of the sampling period indicates that either the infection of this digene persists in wintering offshore fish or that the intermediate host also occurs in offshore waters.

A small number of digenetic trematodes belonging to the family Microphallidae were recovered from a few croakers in the present investigation. Baer (1943) and Stunkard (1960) documented a generalized description of a microphallid life cycle which depicts crustaceans as intermediate hosts and birds as definitive hosts. All immature microphallids recovered were from fish that contained crabs as food items. Thus, M. undulatus may represent only a "temporary" host for this microphallid. In other words, the croaker may either be a paratenic host or a "dead-end" host. In the case of the former, the host is not necessary for the completion of the life cycle but is used as a

temporary refuge and eventually as a vehicle for reaching the obligatory host. It is most likely though that the croaker in this case represents an unnatural host in which the microphallid will develop no further and die. In either case, development to sexual maturity will not occur until the parasite is in the final host.

The knowledge that this microphallid may be utilizing the croaker as a temporary host led to the examination of all microphallid genera which have been reported from the Chesapeake Bay-Beaufort area as metacercariae in crustaceans. These crustaceans which serve as food items for the croaker were examined in great detail. The microphallids recovered in the present investigation may have been in the genera Carneophallus, Microphallus or Megalophallus. Conclusive identification was hampered by the taxonomic uncertainty which surrounds all three genera.

This uncertainty originated when Biquet, Deblock, and Capron (1958) considered the genus Carneophallus to be redundant and reduced it to a synonymy with the genus Microphallus. These authors argued that the lobulation of the copulatory organ was a morphological feature which varied among certain species but it was not significant enough to warrant a new genus. These same investigators insisted on synonymy even though other authorities believed the variety of the terminal genitalia exceeded the limit of a genus (Bridgman, 1969). Cable, Conner and Balling (1960) insisted that the origin of taxonomic relationships could not be satisfactorily based upon adult morphology. These investigators objected to the lumping of heterogeneous groups into the single genus, Microphallus, so they erected the new genus Megalophallus. The morphological



differences that separated this genus from other microphallids was the existence of a complex metraterm and a cup-like male papilla with the male duct opening at the bottom of the cup (Prevet & Deblock, 1970). Present usage appears to support recognition of Microphallus and Megalophallus.

The lobulation and fine detail of the terminal genitalia in the microphallid trematodes recovered in the present study were not visible due to the small number and poor quality of the specimens. Without improved resolution or additional specimens, it can only be postulated that these microphallids belong in either one of two genera: Microphallus or Megalophallus. Specific possibilities include Microphallus nicolli which has been reported in Callinectes sapidus from Beaufort by Deturk (1940) and Megalophallus sp. from the same host.

Up to now, emphasis of this investigation has been placed on seasonality and the indirect life cycles of the Digenea. In most cases, the completion of the complicated life cycles of the Digenea is the result of the final host utilizing the intermediate hosts as food items. In the family Sanguinicolidae, however, food items are not used to transfer the parasite. The life cycle of these trematodes generally includes the development of the eggs to the miracidia stage in the capillaries of the host's gills, the infection of a snail by the miracidium, and the infection of a new piscine host by the cercariae that escape from the gastropod. The cercariae develop into adults within the circulatory system of this final host.

It is evident from the literature that the specific components of most sanguinicolid trematode life cycles is unknown. The sanguinicolid

recovered in the present investigation was an unidentified species of Cardicola. It is apparent from the literature on Cardicola that only two of the species have been separated in marine fish from the western Atlantic. The nearest reports include two Cardicola species from fish captured in the Gulf of Mexico. Cardicola cardicola was recovered from Calamua bajonado by Manter (1947); while Cardicola laruei was reported from Cynoscion arenarius and Cynoscion nebulosus by Short (1953). The taxonomy of Cardicola sp. recovered in the present investigation indicates that this digene possesses a strong but not complete resemblance to C. laruei. A close examination of the Cardicola species from the croaker reveals that it possesses a conspicuous section of the oviduct with an enlarged fusiform chamber apparently utilized for the storage of spermatozoa. Previously, this feature was thought to be unique to C. laruei. The major difference between Cardicola sp. from croaker and C. laruei appears to be in the length of the anterior cecae. Cardicola laruei possesses anterior cecae that are 2 to 3 times longer than in the species recovered from the croaker. This digene may represent a new species but additional specimens are necessary to determine whether additional differences (especially in the genitalia) are present, and to better assess the variability in cecae length.

In contrast to the complicated life cycles of the Digenea, the occurrence of Monogenea on a particular fish species is governed primarily by the prevailing environmental conditions and host specificity. The presence of a physiologically compatible host under the right physical conditions will in most cases ensure the completion of the monogene life cycle. The absence of a monogeneid on a species of fish from which it is known to occur can be attributed to the lack

of contact between infected fish and the rest of the stock or the existence of an environmental barrier to the parasite. Thus, the emphasis on the monogeneids found in this investigation will be placed primarily upon the incidence of new Monogenea and then seasonality.

A review of the literature revealed that 6 monogeneid species, from 5 families, have been reported from Micropogonias undulatus. Three monogeneids were recovered in the present study but only two have previously been reported from the Atlantic croaker. The presence of the third, Neopteriotrematoides avaginata, is not only a new host and locality record but its occurrence has potential significant ecological and systematic implications on Micropogonias species found in the western Atlantic.

Macrovalvitrematoides micropogoni is a monogeneid which has been shown to be specific for M. undulatus. It was originally described as Taiga micropogoni by Pearse (1949), redescribed by Hargis (1956), and since that time has been found in croakers ranging from the northern Gulf of Mexico (Joy, 1972) to the Chesapeake Bay (Kingston et al., 1969). Large numbers of this parasite were recovered from all sizes of croaker captured in both oceanic and estuarine habitats during this study. This distribution demonstrates that M. micropogoni possesses a wide tolerance not only to salinity but also temperature.

Absonifibula bychowski is the representative of a monotypic genus in the subfamily Absonifibulinae described by Lawler & Overstreet (1976). These same investigators reported an incidence of infection of this monogeneid of 2.8% in young of the year and adult fish combined. The mean number of parasites found in that study was reported to be 3.8 indivi-

duals per fish. Lawler & Overstreet (1976) noted that the incidence of infection was considerably higher in young of the year fish and that the total prevalence and intensity appeared to be directly related to temperature. These same authors reported that James Joy found that 1.5% of 587 croakers were infected with a mean intensity of 1.6 specimens of A. bychowski per fish. In comparison, the results of the present investigation demonstrate that this monogeneid was recovered from 4.2% of the young of the year fish in the present study, but was completely absent in fish greater than 0+ in age. Lawler & Overstreet (1976) postulated that the higher prevalence of worms in young fish may be due to biochemical differences associated with age or differences in population density.

The genus Micropogonias contains a total of five species which are distributed between the tropical eastern Pacific and the western Atlantic. The two species in the western Atlantic, M. furnieri and M. undulatus, are presently considered to be two separate species which exist in two non-intermingling stocks. The northern species, M. undulatus ranges along the U.S. Atlantic and Gulf of Mexico coasts south to the Bay of Campeche, Mexico. The southern species, M. furnieri, is present in the Antilles and along the South American coast.

Taxonomic differentiation of the two species has been a problem ever since the original description of the type species, M. lineatus, by Cuvier (1830). Jordon (1917) first designated M. lineatus Cuvier (= Perca undulatus Linnaeus) as the type-species for Micropogonias. It was later decided that Cuvier's (1830) description could fit both M. furnieri and M. undulatus but through the examination of various

syntypes it was decided that the type species should be M. furnieri (Chao, 1978). Distinguishing characters presently used in the differentiation of these species are based upon the morphology of the sagitta, the color pattern of the fish, and the number of scales in a vertical series from the origin of the dorsal fin to the lateral lines. Micro-pogonias undulatus captured in the southernmost part of their range have demonstrated an intermediate morphological form of the sagittae. The remaining small difference between these two species has led to serious speculation that a synonymy should be established or at least that these two fish should be considered subspecies (Chao, pers. comm.).

The occurrence of Neopteriotrematoides avaginata on M. undulatus is significant because this monogeneid was previously recorded only from M. furnieri captured in the coastal waters off Brazil. The occurrence of this parasite on M. undulatus is further evidence that the question of a synonymy between Micropogonias species should be further investigated since monogeneids usually demonstrate strong host specificity. A subsequent question raised by the occurrence of this monogeneid in the present study is why other parasite investigations in the south Atlantic and the Gulf of Mexico have never recovered this ectoparasite. A possible explanation includes the existence of a disparate or anti-tropical distribution if the monogeneid was not transferred through intermingling fish stock. Diaz & Johnson (1974) may have misidentified this monogeneid as Pteriotrematoides sp., from Atlantic croakers taken in the coastal waters of North Carolina. This report could not be checked due to the existence of only an abstract with no figures or drawings. It is clear that the keys available at that time would erroneously identify N. avaginata as Pteriotrematoides.

In the present study, N. avaginata was much less abundant in croakers collected in the estuarine habitat and in those migrating out of the Bay, than in incoming fish. Possible reasons for this trend include the influence of the changing physical environment and competition from other monogeneid species. Detrimental competition from M. micropogoni was not readily evident from the data but it was observed that M. micropogoni maintained a high level of incidence in all sizes of the Atlantic croaker while the incidence of N. avaginata decreased with the progression of the summer.

The aspidogasterid, Lobatostoma ringens was first reported as Aspidogaster ringens from M. undulatus by Linton (1905). Eckman (1932) erected the genus Lobatostoma and established a synonymy between L. ringes and Cotylogaster chaetodipteri (MacCallum, 1921). This aspidogasterid has been reported to range from North Carolina to Argentina (Yamaguti, 1963a) therefore, the occurrence of L. ringens in the present study is a new locality record and an extension of this range.

Hendrix & Overstreet (1977) stated that this aspidogasterid has been reported from 13 different piscine hosts from 8 separate families. This list includes three Micropogonias species captured in western Atlantic waters. This report is contrary to the present belief that only two Micropogonias species exist in the western Atlantic (Chao, 1978). The occurrence of L. ringens in M. furnieri (Nahhas & Cable, 1964) and M. opercularis (Suriano, 1966) should be regarded as reports from synonymous hosts.

Considerably uncertainty exists in the knowledge on the life cycles of the Aspidogastrea. Noble & Noble (1971) seemed to put it best by stating that the development of aspidogastroids is "basically direct". These same authors defined direct development as the maturation of an organism from the egg to adult stage within the same host. The problem is that the eggs of some aspidogasterids enter and develop into egg carrying individuals in a bivalve host while others, like L. ringens, are believed to require a teleost for the completion of the life cycle (Overstreet & Heard, 1978). It is speculated that the infected bivalve is consumed by the fish and because L. ringens possesses the ability to withstand digestion results in the attachment of this parasite to the gut wall. Noble & Noble (1971) speculate that this process may have been the first evolutionary step in the initiation of a second host in the Digenea. Huehner and Etges (1977) demonstrated that this is not the general rule for all aspidogastroids in their documentation that the life cycle of *Aspidogaster conchicola* takes place within one snail host.

Hendrix & Overstreet (1977) report that juvenile L. ringens have been found in two subspecies of the clam, Donax roemerii. These same authors report the occurrence of pre-adult and adult *L. ringens* in fish which fed on Donax roemerii protracta. Hopkins (1958) reported an aspidogastroid in Donax roemerii roemerii which Sparks (1960) considered to be L. ringens. Both species of *Donax* are known to occur on beaches which demonstrate high energy and high salinity characteristics.

Results from the present study reveal that both preadult and adult L. ringens were recovered from M. undulatus throughout the later months

of 1978. The known intermediate hosts for this species was not identified in the gut contents of the croaker but it is known that *Donax* are limited in their distribution in the region of the Chesapeake Bay to the Bay mouth (Wass et al., 1972). This limited distribution in conjunction with the fact that many of the young of the year fish were infected, raises some question concerning the source of *L. ringens*. It was previously shown that these young of the year fish spend their first year of existence in the Bay, where presumably the intermediate host of this aspidogastroid does not exist. Possible explanations concerning infections in younger fish appear limited to the movement of juveniles to the mouth of the Bay or a different intermediate host which can survive under estuarine conditions. Further investigation is necessary.

Wardle & McLeod (1952) stated that the knowledge concerning the development and life cycle of tapeworms has accumulated at a significantly slower rate than the data relating to their general anatomy. Past reports of cestodes recovered from *M. undulatus* reveals that this sciaenid plays an important intermediary role in the completion of several cestode life cycles. Five metacestode trypanorhynchys comprising three separate families have been reported from the Atlantic croaker. For the sake of convenience and clarity the cestodes recovered in the present study have been described utilizing a classification system established by Freeman (1973). The terminology used in this system of cestode ontogeny eliminated the majority of past confusion associated with names that were rooted in the history of their origin and application.



An unidentified species of the genus Pterobothrium, a tentaculo-pleurocercus, was recovered from the mesentery and gut walls of the croaker. Three species of this genus have been previously reported from Micropogonias but considerable confusion surrounds both the taxonomic status of these parasites and the hosts in which they were found.

The genus Pterobothrium Diesing, 1850 has been synonymized with Synbothrium Diesing, 1850 and Syndesmobothrium Diesing, 1854. Pterobothrium macrourum is the type species of the genus and has been reported in M. undulatus from Montevideo, Uruguay (Yamaguti, 1959). This host is now believed to be M. furnieri based on the established distribution of croaker species by Chao (1978). Pterobothrium heteracanthum was initially reported from Brazil in M. lineatus which is also presently believed to have been M. furnieri. Pterobothrium heteracanthum has subsequently been reported from M. undulatus but further taxonomic work is needed on this species (Overstreet, 1977). Pterobothrium filicolle has also been reported from M. undulatus captured in Beaufort, N.C. and the coastal waters in Texas. Chandler (1935) originally identified this cestode as Gymnorhynchus gigas which he later (1942) reconsidered to be P. filicolle.

Data in the present investigation indicate that Pterobothrium sp. was essentially absent in young of the year croakers. These results are similar to those reported for other trypanorhynch species by Overstreet (1977). He attributed the absence of these parasites in young fish either to the unavailability of intermediate hosts or the vulnerability and subsequent death of fish which are infected with this parasite.

No attempt was made in the present study to evaluate the seasonality associated with the occurrence of these encysted metacestodes. These trypanorhynchs are considered persistent parasites which are in no way affected by a changing physical environment. Since young croakers did not contain this parasite it can be postulated that the intermediate host is oceanic in nature or that it is not a part of the croaker diet until the fish reach a larger size.

The two tetraphyllidean metacestodes, recovered from the alimentary tract of the Atlantic croaker, possess larval characteristics that have been surrounded by uncertainty in the past literature. This uncertainty is the direct result of most past investigations reporting almost all tetraphyllidean metacestodes under the "catch-all" categories of Scolex pleuronectis Muller, 1788 and Scolex polymorphus Rud, 1819. Thus, the result of these categories has been the clumping of several different larval tetraphyllideans under the same name. Yamaguti (1934) caused further confusion through his unrecognized attempt to differentiate these "catch-all" categories. As a result of this confusion, the larval tetraphyllideans recovered from the alimentary tract of the croaker were simply described and labelled species "A" and "B".

It was found that only one of the two larval tetraphyllideans was recovered in large enough numbers to allow any conclusions to be made regarding seasonal occurrences. Species "A" demonstrated a lower incidence in croakers captured in the estuarine habitat. An explanation for this trend includes a change in the feeding habits of the croaker and the possible exclusion of the intermediate host by the physical parameters of the estuary.

The remaining cestode recovered in the present study was a pseudophyllidean. The seven specimens recovered from M. undulatus displayed maturation states which ranged from a metacestode to a "pre-adult" with a segmented strobila and genital primordia. It is speculated that the absence of gametogenesis indicates that the croaker is not a final but possibly an intermediate host. A review of the cestodes reported from possible final (elasmobranch) hosts in the Chesapeake Bay and offshore waters provided no assistance in further identification of these cestodes. It is apparent that additional specimens of better quality are necessary for speculation into the life cycle of this cestode and the role that is filled by the croaker.

Dollfusentis chandleri Golvan, 1969 is the most prevalent as well as taxonomically confused endoparasite found in the croakers of the present study. This state of confusion has surrounded this acanthocephalan ever since Linton (1891) erroneously considered this parasite a subspecies of Echinorhynchus pristis. Linton's variant, E. pristis tenuicornis, was later redescribed and recognized as a distinct species, Rhadinorhynchus tenuicornis, by Van Cleave (1918). The unfamiliarity of this author with zoological nomenclature procedure resulted in additional confusion when several investigators (Meyer, 1932; Chandler, 1934) attributed this "new species" to him. Support for this new species seemed to appear when Chandler (1934) and Van Cleave & Linicome (1940) raised no question as to the propriety of assigning tenuicornis to the genus Rhadinorhynchus. The combination of improved optics and scrutiny of the male genital area lead to the transfer of this species to the genus Telosentis by Van Cleave (1947). Specimens of Telosentis tenuicornis have been reported from M. undulatus both in the Gulf of Mexico (Chandler,

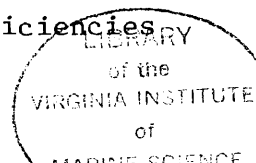
1954; Bullock, 1957) and the Chesapeake Bay (Huizinga & Haley, 1962). A total contradication of all past work done on this species resulted when Cable and Linderorth (1963) stated that this acanthocephalan was neither a species of Telosentis not what Linton described as Echinorhynchus pristis tenuicornis. Golvan (1960) erected Dollfusentis nov. gen. and applied the new name, Dollfusentis chandleri, specifically to the specimens described from Galveston Bay by Chandler (1934). Golvan (1969) described four separate species but Bullock and Mateo (1970) considered D. longispinus (Cable & Linderorth, 1963) a synonym of D. chandleri. At the present, taxonomic problems continue to exist between specimens of D. chandleri taken from different geographical areas. Bullock (pers. comm.) considers all specimens taken from the Gulf of Mexico to consist of one species. This same investigator believes that specimens from the western Atlantic and the Gulf of Mexico can be quantitatively differentiated through the use of anterior trunk spines, probosis hooks, and genital spines. Whether these statistical and quantitative characters are a sufficient basis for the formation of a new taxonomic group is still under question. Thus, due to the existence of this uncertainty, the specimens recovered in the present study, should be referred to as Dollfusentis chandleri (?) (Bullock, pers. comm.).

Investigation into the life cycle of D. chandleri was first attempted through the work of Huizinga & Haley (1962). These investigators found that the spot, Leiostomus xanthurus, acquired this acanthocephalan during their summer residence in the Chesapeake Bay. Overstreet (1969) also noted that D. chandleri occurred primarily during the summer months but that many individuals apparently remained in M. undulatus an entire year. Due to the longevity of this parasite, Overstreet (1969) stated

that patterns of incidence in a specific year class of a host had more meaning than those of the total sample.

Results of the present investigation indicate that D. chandleri has a strong seasonal pattern of incidence. Incoming migratory fish displayed a considerably lower incidence and intensity than those fish captured in the bay. In contrast to Overstreet (1969), the total picture of all age classes did seem to demonstrate a consistent increasing trend of incidence throughout the summer. Data were not available for all sizes of young of the year croakers but it was evident that these fish acquire D. chandleri not only at a higher level of incidence than the larger fish but more often as the only parasite in the alimentary tract. Buckner et al. (1978) established the intermediate host of this acanthocephalan in the northern Gulf of Mexico as two species of amphipods. A strong correlation can be shown in the present study between the food preferences of young fish for these crustaceans and the high incidence of this parasite. It is postulated that the lower levels of infection in larger fish are due to the decreased preference for the intermediate host as a food item and most importantly the unavailability of this host in the offshore winter habitat.

The study of a possible detrimental relationship between a parasite burden and the condition of a fish is not new in parasitological investigations. Meyer (1954) generally stated that parasites can kill or weaken a fish. Sindermann (1970) summarized the known detrimental effects of parasites on fish as stunting of growth, emaciation, sterility and mortality. Croakers collected in the Chesapeake Bay in this investigation demonstrated no physical evidence that any of these deficiencies



were present. Mulligan (1972) did show that a gastro-intestinal helminth burden could cause some derangement of function in the gut. These disturbances included impaired digestion, malabsorption, abnormal losses of endogenous metabolites into the gut and anorexia. Large gastro-intestinal burdens postulated to be capable of these impairments were noticeably present in the croakers less than 200 mm in length. These helminth burdens consisted almost exclusively of large numbers of the acanthocephalan, D. chandleri. The sheer number of these parasites can result in occlusion of the gut and weakening of the host. Acanthocephalans are also capable of mechanical damage to the intestine (Prakash & Adams, 1960; Venard & Warfel, 1974) which could interfere with food absorption and cause a debilitating effect on the host. It was postulated that the burden would have a weight reduction effect on the fish which would result in a reduced coefficient of condition. A conclusive determination of whether a reduced condition did result from the parasites was not possible due to the small number of uninfected fish and the requirements of the test which allow comparison of fish only within 10 mm increments. A large sample size is necessary not only for statistical purposes but because many variables influence the computation of this coefficient.

Serrasentis socialis, like D. chandleri, did not have detrimental effects on the Atlantic croaker. This acanthocephalan was originally named Echinorhynchus socialis until Linton (1889) reported it as E. sagittifer and VanCleave (1923) claimed it was synonymous with Serrasentis socialis. This acanthocephalan, unlike D. chandleri, was not recovered as an adult from the alimentary tract of the fish. Cystacanths of this species were found in the mesenteries and it is

believed that M. undulatus represents only a paratenic host in the life cycle of this parasite. Baer (1951) described a paratenic host as any organism which serves as a "storage depot" or temporary refuge for a parasite. Cheng (1973) states that this type of host is not necessary for the completion of the life cycle but it is quite often used as a vehicle for reaching the definitive host. Yamaguti (1963b) reported that adult S. socialis have been reported from the cobia which in this case can be assumed to obtain this parasite by feeding on infected fish like the croaker.

Serrasentis socialis, unlike many of the parasites in this investigation, does not exhibit any seasonality of incidence because it is a persistent parasite that remains viable while the host migrates from one area to another. It cannot be determined where or when this parasite is acquired by adult fish without a year round sampling program of all age classes of croakers. A rough estimate of the period of time a cyst has been in a fish can be determined by the degree of fibrosis associated with the encapsulated worm. Very little fibrosis was demonstrated in the specimens recovered in the present study. Serrasentis socialis was absent in young of the year fish, perhaps because the invertebrate host is rare in the bay or is rarely consumed by the small fish.

Ergasilus labracis is a cyclopoid copepod which has been previously reported only on the striped bass (Morone saxatilis) and white perch (Morone americana) in the Chesapeake Bay (Paperna and Zwerner, 1976). Infection intensities up to 2757 copepods per fish were reported from four age classes of striped bass. These same authors reported that

E. labracis demonstrated a definite seasonal pattern of abundance and that infections of high intensities often caused gill hyperplasia. Croakers were not examined for this condition in the present investigation because of the small number of copepods per host. No seasonal pattern of abundance was evident for E. labracis in the present investigation due to the small number of infected individuals, but E. labracis was recovered from adults as well as young of the year fish.

Earlier investigations have reported several different species of Ergasilus from the Atlantic croaker. Causey (1953) reported E. nanus van Beneden, 1870 from M. undulatus taken in the northern Gulf of Mexico. This occurrence is viewed with considerable doubt based on the inadequate description and the complete absence of this copepod in any other reports from North American waters (Roberts, pers. comm.). Roberts identified several specimens of E. lizae taken from four individual M. undulatus collected in the Gulf of Mexico by Overstreet. It is postulated by Roberts (pers. comm.) that Causey's specimens were also E. lizae.

The majority of copepods which compose the order Lernaepodoidea are fish parasites which are only vaguely understood because many of the species have not been rediscovered or redescribed since the time of their original description (Ho, 1977). No seasonal pattern of abundance or other life cycle information on Clavella inversa can be determined in the present investigation due to the low level of incidence in M. undulatus. The sole occurrence of this copepod on incoming croakers has lead to the hypothesis that C. inversa is restricted to the oceanic habitat. Further investigation is necessary to confirm this speculation.



The genus Argulus has been a focus of taxonomic confusion throughout the scientific literature. The number of species which have been described or reported from U.S. coastal waters has varied in the literature from a maximum of 31 to a low of 23 species. Meehan (1940) established the first recognized key to the genus and listed 23 separate species. Wilson (1944) raised the number of valid species to 31 with his disagreement with eight synonymies established by Meehan. Cressey (1972) supported Meehan's earlier findings and again reported a total of 23 recognized species.

The low incidence of A. bicolor did not allow for the analysis of data trends in the present investigation. It should be noted that the time of occurrence on the croakers did coincide with a reported seasonality for A. bicolor in the Chesapeake Bay by Paperna & Zwerner (1976). These same authors documented the occurrence of a pathological condition resulting from the presence of large numbers of this branchiuran. "Argulosis" in striped bass resulted in skin ulceration characterized by erosion of the epithelium and extensive proliferation of the underlying dermis. Croakers were not examined for the presence of this lesion in the present study due to the small number of A. bicolor recovered.

Lironeca ovalis, like the other parasitic crustacea found in this study, was rarely encountered. The few occurrences on croakers did coincide with the seasonality reported by Paperna & Zwerner (1976) in the Chesapeake Bay.

The marine leeches of the eastern U.S. until quite recently have been a neglected group of organisms due primarily to the bewildering taxonomy of the members. Most early species descriptions were ambiguous

reports which lead to the perpetuation of nomenclatural confusion (Sawyer et al., 1975). This is exactly the case for the leech recovered in the present investigation. The vague original description of Cystobranthus vividus by Verrill (1872) and Moore (1898) lacked any mention of internal anatomy which in conjunction with the loss of type material has resulted in a variety of synonymous names in the literature. Sawyer & Chamberlain (1972) described a supposed new leech, Calliobdella carolinensis which was later synonymized with Cystobranthus vividus by Sawyer et al. (1975). These authors reassigned this species to the genus Calliobdella as C. vivida (Verrill, 1872).

Calliobdella vivida has been previously reported from the Chesapeake Bay (Wass et al., 1972) but its occurrence on M. undulatus is a new locality record for this host. Sawyer & Hammond (1973) reported that this leech demonstrated a seasonal occurrence which is closely correlated with cooler water temperatures. These authors reported that adult leeches reached their greatest abundance from December to May. Adult leeches were shown to breed in the late spring and disappear with the onset of warmer water temperatures.

Calliobdella vivida recovered in the present study demonstrated a seasonal pattern of abundance which differs from one part of the life cycle as previously understood. Small juvenile leeches (7.6 mm - 10.1 mm) were found in late September and October of the 1978 sampling period. Trawl catches during this period were closely examined but no other specimens were seen on a variety of examined hosts. The appearance of these juvenile leeches is much earlier than that reported by Sawyer & Hammond (1973). Further work seems necessary to determine when the majority of the leeches hatch and appear on hosts.

Sawyer & Hammond (1973) postulated that C. vivida was probably a vector for either hemogregarines or hemoflagellates due to the recovery of blood parasites from other blood-sucking piscicolids (Becker & Katz, 1965a, b; Putz, 1972). These authors proposed that C. vivida was the probable vector for Haemogregarina brevoortiae reported in menhaden from Florida (Saunders, 1964). The hemoflagellate, Trypanoplasma bullocki, has been shown to utilize C. vivida as a vector in the infection of up to nine piscine hosts in the Chesapeake Bay (Bureson, pers. comm.). No parasitic protozoa were seen in the blood of a group of M. undulatus sampled during the present investigation.

Past parasitological investigations have reported two separate nematode genera (Spirocamallanus & Thynnascaris) from the alimentary tract of M. undulatus (Joy, 1974; Norris & Overstreet, 1975). There appears to be no report of encysted larval nematodes occurring in the mesentery of the Atlantic croaker. Thynnascaris sp. was found encysted in the present investigation and it is speculated that the croaker serves as an intermediate or paratenic host for this species. Overstreet & Heard (1978) reported finding Thynnascaris reliquens almost always as immature individuals but from the gut of M. undulatus.

A seasonal pattern of abundance was evident for Thynnascaris sp. but like other encysted parasitic larvae this nematode is considered a persistent parasite. The trend of decreasing incidence of this encysted nematode with season seems to have no reasonable explanation. In this case the change of incidence is not the result of the migration into different geographical areas. It should be noted that this nematode infected a negligible percentage of young of the year fish. Apparently

the intermediate host is either not very abundant in the Bay or croakers are either unable or do not prefer it as a food item.

Mature specimens of Goezia sp. were recovered from the alimentary tract of the Atlantic croaker. No conclusions could be made regarding the seasonality of this parasite because of the low incidence of infection. It is postulated that these specimens may be Goezia annulata but additional samples of better quality are necessary for confirmation. The occurrence of this nematode in M. undulatus is a new host record for the genus.

#### Statistics and the Comparison of Parasite Communities

The ecological principles which govern a biocoenosis of free living organisms are in many ways quite similar to those which can be applied to parasites. Odum (1971) defined ecology as consisting of two subdivisions: autecology and synecology. The first category deals with the study of the individual organisms or an individual species. Life histories and behavior as a means of adaptation to the environment are emphasized in autecology. The latter category is concerned with the relationships between the members of the biocoenosis and the environment. Dogiel (1970) demonstrated that parasitology can be defined in a similar matter. One division is concerned with the study of the relationship between individual parasites and their host and the other is concerned with the conditions influencing the parasite fauna of a particular host species as a whole. Underlying these studies is the basic concept of parasites as animals whose entire environment is furnished by other living organisms. Pavlovski (1934) termed this relationship as parasitocoenosis, and pointed out that the environment of parasites is of dual

character. It is not merely the host but also the host's environment that forms the environment of the parasite. The parasitocoenose is a biological entity that reacts and changes with both environments.

In general, the factors that determine the constituent species of a parasite community seem to be best described by the interdependence that exists in the three epizootiologic variables described by Snieszko (1973). Snieszko stated that the outbreak of diseases in fish is governed by the interaction of the host, pathogen, and the environment. Snieszko graphically presented these variables as circles which when intersected produce conditions that are favorable for an outbreak of disease. Kabata (1963) stated that a parasitological "external triangle" also exists and consists of the prevailing environmental conditions, the characteristics of the host, and the interrelationships between the members of the parasitocoenose. A change in any one of these three components may displace the balance and preclude a parasite from both entering and remaining in the host.

Kabata (1963) demonstrated that a change in the environmental conditions will disrupt the balance of the three factors from area to area. This in turn produces a difference of parasite infections between populations of the same fish. Based on this premise, it is believed that the difference in the incidence and intensity of parasites in the croakers migrating from the ocean to the estuary may be due primarily to the change in environmental conditions. Specific reasons considered responsible for the change include the tolerance of physical parameters, alteration of food habits, and the dependence on specific invertebrates for completion of life cycles. The second epizootiologic variable, the

host, was considered to be a constant in the present study because of the separation of fish into size groups. Thus, the only remaining variable that may be influential in an alteration of the parasitocoenose are the interspecific interactions of the parasites.

Interspecific interactions between members of the parasitocoenosis take place in one of two fashions: interactive enhancement or competition (Hobbs, 1979). Interactive enhancement (a positive relationship) occurs when species pairs are found concurrently more often than by chance. Reasons for this type of interaction include: mutual requirements at the infective stage, similarities in life cycles, or similar environmental requirements outside the host. Cole (1949) proposed that a positive association between two species could be determined through an examination of the frequency of co-occurrence in a series of samples. A negative association between parasites can be the result of one of a variety of factors. These factors include: dissimilarities in a life cycle, immune responses of the fish, and competition. This latter factor was examined in the present investigation and can be separated into the categories of either interference or exploitation competition (Miller, 1967).

Competition by definition occurs when two or more organisms interfere or inhibit one another. Interference competition is considered to be a direct confrontation with the result being either the reduction of numbers of one parasite or the exclusion of one species from the host. Gause's principle states that this competitive exclusion is one of two results that can occur when species occupy overlapping niches (Odum, 1971). The second result is another negative association known as

exploitation competition. This interaction can be described as a "scramble" (Nicholson, 1954) by competing species (or individuals) with equal access to a limited resource (the host). The competition is manifested by reduced weight and length of individuals or interactive site segregation (a changed distribution within a host).

Planks (1976) stated that niche overlap need not in all cases lead to competition unless resources are in short supply. This competition may influence niche breadth (the sum total of the variety of different resources exploited by the parasite) by either an expansion or contraction depending again upon resource availability. This change in niche breadth will result in an alteration of the parasite distribution within the host. Site preference was not examined in the present study but it is known that the distribution of helminths may be of three types: random, infradispersal, and supradispersal (Hirsch & Gier, 1974). Infradispersal or a more evenly spaced distribution results from interference competition while supradispersal or clumping is the result of exploitation. All three distribution patterns have been found in parasitological investigations on mammals (Hirsch & Gier, 1974).

An analysis of the results indicated that neither a strong positive or negative association was evident for any one pairing of helminths. Statistical tests demonstrated that there were no cases of competitive exclusion. Three species pairs were found concurrently more often than by chance. Two of these pairings were attributed to the bias of the low incidence of O. vitellosus while the other one was possibly due to similarities in life cycles. The failure to find significance indicated that helminth infections did occur independently of one another. A

significant result that the absence or presence of a parasite has an effect on the level of infection of another parasite was evident in only one helminth pair. The results of the non-parametric tests in all cases but one call for the acceptance of the null hypothesis that the samples come from populations with the same distribution. The one significant association included a reduced level of infection of O. fimbriatus in the presence of D. lecostomi. Additional samples and additional information on the life cycle and host specificity are necessary before any conclusions could be made regarding this association.

Community structure is referred to as the complex of individuals belonging to the different species in an ecosystem (Wilhm & Dorris, 1968). Cloutman (1975) expanded on this definition by describing parasite community structure as the complex of individuals belonging to different parasite species inhabiting a host. It is often necessary to reduce the large amounts of raw data on community structure into ecological indices that simplify the study of community dynamics. The ecological concepts that are important in the study of community structure include: diversity, dominance, and similarity.

Odum (1971) recognized that species diversity is made up of two components: equitability (evenness) and species richness (variety). Equitability is the apportionment of individuals among the species while species richness represents the ratio of the number of individuals of each species to the total number of individuals. The Shannon Index ( $\bar{H}$ ) of general diversity is widely used in the study of community structure but combines the results of the separate diversity components. Cloutman (1975) indicated that because of epizootiological importance, size is a



significant attribute of a parasite community. Thus, it was determined that diversity should be separated into the respective components that can be computed from variations of the equation for Shannon's index.

It is apparent from the diversity values presented in the monthly sampling format that differences exist between the two indices and that individual diversity is inversely related to redundancy (dominance). It was found that croakers entering the Bay in the spring had a parasite community large in size but was dominated by the larval cestode (Tetraphyllidean sp. A). This larval cestode was found in such large numbers that the computed mean number of parasites/fish was deceptively large. It was originally hypothesized that croakers wintering offshore would have parasite communities small in size because of reduced feeding, but this was not the case due to the enormous numbers of this larval cestode. The mean number of parasites/fish dropped sharply with the progression of the summer because of a severe reduction in numbers of this larval cestode. In contrast, community diversity which is a function of size and equitability increased to a maximum in the June (York River) sample. It is believed that this was due to the increased number of species and a function of higher equitability. It was postulated that the parasite community carried into the Bay from offshore was added onto by parasites with estuarine life cycles and the number of species in the community reached a maximum in the June (York River) sample. From July onwards the offshore parasites began to disappear and the size, but not necessarily the equitability, of the community continued to decrease. Individual diversity is independent of sample size, and was, therefore, insensitive to changes in the number of individuals in the community. The values for this index increase by small amounts with

the progression of the summer with the exception of the September (York River) sample. This trend is an indication that no one species was dominant. The low individual diversity of the September (York River) sample is attributed to the large numbers of D. leiostomi in several fish taken in that sample. This same digene, an addition to the copepod E. labracis, was responsible for the increase in the mean number of parasites/fish and community size in the October (Chesapeake Bay) sample. Unfortunately, not all of the monthly samples can be easily explained. The May (York River) sample displayed an unusually small number of parasites/fish as well as a reduced value from community diversity. Most samples taken in 1977 appeared to demonstrate similar trends to those of 1978 except that the total number of species recovered and the size of the community were considerably smaller in 1977. It is also important to note that croakers less than 200 mm also displayed smaller communities with a small number of species, but most importantly that the values for dominance were very high. Dollfusentis chandleri was recovered in large numbers from juvenile croakers.

The principle that a population of fish living in a given area will acquire parasites characteristics of that area is the basis for the concept that parasites can be utilized as biological tags (MacKenzie, 1975). A variety of parasites including both endo- and ectoparasites, have been used as tags to distinguish separate oceanic stocks of fish, determine a geographical origin or nursery area, as well as aid in the determination of the evolutionary history of the species (Gibson, 1972; Lubieniecki, 1977; Margolis, 1965). Kabata (1963) and Sindermann (1961) list several requirements that are necessary if a parasite in a particular stock of fish is to be used as a biological tag. It was found that the fulfill-

ment of these requirements is questionable in the present study mainly because it is believed that all M. undulatus north of Cape Hatteras are one intermingling stock of fish (Musick, pers. comm.). Haven (1959), with limited returns in a traditional fish tagging study, demonstrated that croakers migrate around the cape but generally do not migrate any further south. Thus, the alteration of the parasitocoenose in one migrating stock of fish like in the present study confirms the principle that fish acquire parasites characteristic of a particular area but in this case cannot be utilized as biological tags.

The similarity of the parasite communities recovered from the monthly samples of croakers taken at the mouth of the Bay and the York River were compared through the computation of Sorrenson's index and numerical classification. Sorrenson's index reflects the qualitative similarity between monthly samples based on the ratio of the number of species shared to the total number of species. The values of this index compared on a monthly basis demonstrated that a decreasing trend of similarity for two categories of parasites was associated with the migration of the croaker and the progression of the summer. These categories included the Digenea and all parasites.

The Digenea were singled out for this comparison because of their dependence on specific intermediate hosts for the completion of their life cycles. The change in community similarity can be directly attributed to the absence or presence of particular species but can be explained only through an understanding of the constituent life cycles. Lepocreadium setiferoides and S. tenue demonstrated a large increase of incidence in samples taken later in the season. It was hypothesized that

these digenes have life cycles that operate in the Bay. Four of the remaining eight Digenea demonstrated a decrease of incidence through the summer: L. microstomum, Hemiurid sp. A & B, and O. fimbriatus. These data support the hypothesis that their life cycles operate in the off-shore habitat. The remaining four Digenea did not demonstrate an increase in incidence for either habitat but D. leiostomi does show a very high incidence in smaller croakers. These smaller fish possess a parasite community that has a low similarity to the parasitocoenosis of croakers caught in the spring and a higher similarity to those leaving the Bay in the fall. This data supports an earlier assumption that these smaller croakers remain and feed in the Bay their first year of existence and thus would acquire parasites characteristic of the Bay.

The trend in similarity among communities of all parasites was not nearly as definite as that of the Digenea. The influence of inconsistently occurring encysted parasites and those with direct life cycles caused large variations in the similarities of adjacent months. The parasites that displayed a decrease of incidence through the summer include: N. avaginata, Pterobothrium sp., Tetraphyllidea sp. A & B, Pseudophyllidea sp., S. sociallis, and Thynnascaris sp. Dollfusentis chandleri demonstrated an increase of incidence that supported past findings that this acanthocephalan has a life cycle utilizing estuarine hosts. The remaining parasites displayed no recognizable trend of incidence because of rarity or constancy of occurrence. All monthly data, no matter how small the sample size, were utilized for this qualitative index. It must be recognized then that this index is considered a weak indication of similarity. Thus, the parasites can be described by their trends of incidence but only speculation can be made regarding the ecology of parasites.

Numerical classification is a multivariate analytical technique that illustrates faunal transitions through an expression of similarity in species abundances and distribution patterns. This analysis utilized in conjunction with life cycle information presents what may be considered a more complete "picture" of the interactions of parasites in the migrating croaker. Boesch (1977) believes that numerical classification and diversity indices can be complementary and should be used together in the interpretation of total community structure. This is particularly pertinent to the comparisons of parasite communities from a single host species because until now no parasite investigation has utilized numerical classification. Comparisons in past research have been made by the computation of diversity indices (Holmes and Podesta, 1968; Cloutman, 1975; Esch et al., 1979) and a qualitative index of similarity (Stone and Peace, 1978). An index of species diversity, in the sense of species richness or the number of species in a community, is important to the ecological problem in the present investigation but possesses severe practical limitations. Boesch (1977) points out that this index summarizes community structure through one parameter. Thus, there exists a drastic reduction and loss of information. This loss of information occurs because the species in the community are treated strictly as numerical entities. In contrast, numerical classification simplifies the patterns of multispecies distribution and bases comparisons on the identity of species in the collections.

The normal classification of this analysis separated the collections or stations into three groups based on seasonality as well as age of the host. Figure 2 demonstrates that one group consists of collections containing only fish less than 200 mm in length, while the other two groups

are larger fish separated by time of capture. These divisions clearly support the following two hypotheses: first, that the food habits and general life histories of fish of different size lead to the acquisition of different parasites and second, that fish from different geographical areas or habitats possess different parasites.

A close examination of the hierarchy of collections (Figure 2) revealed two apparent discrepancies in the formation of collection groups. The first involved the formation of collection group I from two constituent groups that displayed a very low value of similarity. This was a good example where the variable stopping rule was necessary for the formation of one collection group. Collections Y861 and Y771 contain 76% of the juvenile croakers collected in the present investigation. It was determined that these collections displayed a low similarity to collections Y751 and Y851 because of the low incidence of L. seterferoides, O. fimbriatus, E. labracis, and A. bychowski in the former collections. It was reasonable to assume that, since these parasites displayed a very low incidence, they would rarely appear if at all in the collections with the small number of croakers. It was determined that all collections contained parasite communities that were characterized by a small community size dominated by D. chandleri. It was concluded that the variable stopping rule should be used to form one collection group.

The second apparent discrepancy in the formation of collection groups was the placement of collection Y822 in collection group III. This collection was an exception to the rule that larger fish are separated by time of capture. The explanation for the placement of this May collection into the group of later samples is that it represented a misclassification. It was determined that, since the

constituent species of the parasitocoenosis would gradually change in the monthly samples and not display radical differences of incidence or intensity, an intensely clustering strategy was necessary to group the most similar entities in the numerical classification. Boesch (1977) pointed out that the intensity of a clustering strategy is characteristically associated with particular types of error in numerical classification. An intensely clustering strategy like Canberra metric, is prone to misclassifications while a weakly clustering strategy is prone to non-classifications. A misclassification can be defined as an entity which is placed in one group by numerical classification but would improve within group homogeneity if it were placed in another (Boesch, 1977). Misclassifications are frequent in numerical classification that utilize space-dilating hierarchical methods and are usually the result of an early fusion in agglomerative clustering in which an entity resembles only one member of the group (Boesch, 1977). These misclassifications may be detected through one of two methods: the examination of the interentity resemblance matrix to uncover entities that have a higher resemblance to another group than the one in which classified and the rearrangement of the original data matrix by collection and species groups as determined by the normal and inverse classifications. The interentity resemblance matrix demonstrated that collection Y822 displayed the greatest similarity with collection C862 but was also more similar to every member of collection group II than collection group III. Thus, it can be assumed that collection Y822 is a misclassification.

Lambert and Williams (1962) described nodal analysis as a method that describes and interprets the dense cells or "nodes" of the data

matrix. This analysis was little help in the identification of a misclassification in the present study because of the criticism that the necessary reallocation or subjective rearrangement of entities nullifies the objectivity of the analysis (Boesch, 1977). Nodal analysis did assist in the ecological interpretation of the numerical classification. The inverse classification interpreted via the two-way tables demonstrated that the differences in collections were due to shifts in species occurrence and abundance.

The six parasite groups depicted by the inverse classification were interpreted via the ecological concepts of constancy, fidelity and abundance. These concepts were helpful in characterizing the parasites but could not be used to make conclusive statements about life cycles. The species groups can be summarized as follows: Species group I contains parasites that were ubiquitous in their distribution and relatively constant in their level of infection. Unfortunately, some information was lost in the placement of D. chandleri into this group because the life cycle of this acanthocephalan is known to operate within the estuary. It is also possible that the placement of this parasite in a ubiquitous group may have been influenced by an error in the assumptions of the sampling design. This error is based on whether croakers migrate directly in and out of the Bay or flux between habitats for a period of time. Evidence supporting the possibility of the flux was the occurrence of D. chandleri in the May (Chesapeake Bay) collection and not the April (Chesapeake Bay) collection. This problem was unavoidable because of the inability to obtain winter samples from the ocean.

Species group II demonstrated an increase in the values for constancy, fidelity and abundance from early to late collection groups.



The constituent species of this group were found in the smaller croakers and overall the data further supported the hypothesis that the life cycles of L. setiferoides and S. tenue operate within the Bay.

Species group III demonstrated a small decrease in the values for constancy and fidelity from early to late collections but displayed a very large decrease of abundance. This was an indication that the incidence of these parasites remained the same but the numbers decreased in later collections. The most important constituent species of this group was the larval cestode (Tetraphyllidean sp. A). This parasite was the dominant species in all monthly samples of collection group II. The rapid decrease in the numbers of this cestode radically altered not only the size of the community but the equitability and species richness. Juvenile croakers displayed a very low degree of infection by the parasites in this species groups.

Species group IV was unique because it contained parasites that occurred primarily on fish less than 200 mm in length. The incidence of A. bychowski was found to be restricted to these smaller fish. In contrast, E. labracis was reported from both size categories of croakers with a noticeably larger abundance in the smaller fish (<200 mm). Species group V was characterized by parasites that had a high constancy and fidelity for collection group II. These parasites were also absent from the smaller croakers. This was an indication that either the intermediate hosts were not being eaten by the juvenile fish or as in the case of the ectoparasites, C. vivida and L. ovalis, or that the distribution or abundance of the fish was not favorable for infection. Species group VI was composed of parasites that were absent in smaller fish (<200 mm), displayed a low overall incidence, and were recovered primarily from the

collections taken early in the sampling period. Goezia sp. was an exception because it was also found in collection group III.

The species that played the most important role in the parasitocoenosis of the smaller croaker in collection group I were contained in species group I and IV. The acanthocephalan, D. chandleri, was not only the dominant parasite but in many cases it was the only parasite of juvenile croakers. The monogeneid, A. bychowski, demonstrated an incidence that was restricted to these young of the year fish. The croakers in collection group II appeared to be most strongly characterized by the parasites in species group I, III, V, and VI. Excluding the ubiquitous parasites in species group I, the majority of these parasites demonstrated either a decrease of incidence or intensity through the summer. The larval cestode, Tetraphyllidean sp. A was found in exceedingly large numbers when the croakers entered the Bay in the spring. This parasite was considered to be the dominant species throughout collection group II. Neopteriotrematoides avaginata, Hemiuridae sp. A, O. fimbriatus, and Pseudophyllidea sp. displayed a gradual reduction of infection while L. microstomum and Hemiuridae sp. B disappeared quite abruptly. The encysted parasites (Thynnascaris sp. Pterobothrium sp., and S. socialis) also demonstrated reduced infections in the later samples of croakers even though no reasonable explanation exists. The parasite communities of the croakers in collection group III were mainly characterized by the parasites in species group I and II. Lepocreadium setiferoides and S. tenue displayed increased infections in the later collections and further supported the hypothesis that both possess life cycles that operate in the Bay.

In conclusion, the alteration of the parasitocoenose of the Atlantic croaker can best be described by a summary of the preceding statistics and life cycles. The offshore parasite community was large in size and dominated by a larval cestode. The movement of the croaker into the Bay introduced parasites with estuarine life cycles (i.e. D. chandleri, L. seterferoides, S. tenue) while the absence of the necessary intermediate hosts of parasites with offshore life cycles resulted in a reduction in numbers of parasites like the dominant larval cestode and L. microstomum. Thus, there was a decrease in community size while equitability and species richness increased in the monthly samples. The maximum number of species was found in the June, 1978 sample. Numerical classification separated the larger fish (>200 mm) into two groups but the change in the parasitocoenose was gradual. The outgoing parasitocoenose displayed a high individual diversity as well as equitability in comparison to the parasitocoenose of the incoming fish. The smaller fish (<200 mm) that had never migrated offshore demonstrated a community small in size, with a small number of constituent species dominated by D. chandleri. Most importantly, numerical classification placed the small croaker (<200 mm) into one group. These results confirmed the hypothesis that fish inhabiting separate habitats acquire parasites characteristic of those habitats and that the biology of the host (diet, size, etc.) is significant to the incidence and intensity of parasitism.

# LITERATURE CITED

- Amlacher, E. 1961. Textbook of fish diseases (in German). English translation Conroy, D. A. and R. L. Herman (Eds.). Jersey City, N.Y.: T.F.H. Public., 302 pp.
- Anderson, W. W. 1968. Fishes taken during shrimp trawling along the south Atlantic coast of the United States, 1931-35. U.S. Fish Wildl. Ser., Spec. Sci. Rep. Fish. 520, 60 p.
- Baer, J. G. 1943. Les trematodes parasites de la musaraigne d'eau necomys fodiens (Schreb.). Bull. Soc. Neuchatel. Sci. Nat. 68:34-84.
- Baer, J. G. 1951. Ecology of animal parasites. Univ. Ill. Press, Urbana, Ill. 223 pp.
- Bauer, O. N. 1958. Relationships between Host Fishes and their Parasites. In Parasitology of Fishes. Dogiel, V.A., Petrushevski, G. K., and Polyanski - Editors. T.F.H. Publications N.J. 384 p.
- Bearden, C. M. 1964. Distribution and abundance of the Atlantic croaker, Micropogon undulatus, in South Carolina. Contributions from Bears Bluff Laboratory 40.
- Beauchamp, R. G. (Ed.). 1974. Marine Environmental Planning Guide for the Hampton Roads/Norfolk Naval Operating Area N.O. O.S.P. No. 250 U.S. Naval Oceanographic Office, Dept. of the Navy, Wash., D.C.
- Becker, B. D. and M. Katz. 1965a. Transmission of the hemoflagellate, Cryptobia salmositica Katz, 1951, by a rhynchobdellid vector. J. Parasit., 51:95-99.
- Becker, B. D. and M. Katz. 1965b. Distribution, ecology and biology of the salmonid leech Piscicola salmositica (Rhynchobdellae: Piscicolidae). J. Fish. Res. Bd. Can., 22(5):1175-1195.
- Biquet, P. J., S. Deblock, et E. Capron. 1958. Contribution a la connaissance des Microphallidae Travassos, 1920. (Trematoda) H. Description de deux especes nouvelles du genre Microphallus H. B. Ward, 1901 sens. nov.: M. debuni et M. canchei, parasites intestinaux de Chara driiformes (Charadrii et Lari) des cotes de France. Considerations sur quelques genres de la sousfamille des Microphallinae Ward, 1901 et essai de ele diagnostique des especes du genre Microphallus Ward, 1901 sen. nov. Annales de Parasitologie. 33:391-444.

- Boesch, D. F. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. *Mar. Biol.* 21:226-244.
- Boesch, D. F. 1977. Application of Numerical Classification in Ecological Investigations of Water Pollution. *Ecol. Res. Series* EPA 600/3-77-033. 115 pp.
- Bridgman, J. F. 1969. Life Cycles of Carneophallus choanophallus N. sp. and C. basodactylophallus N. sp. (Trematoda: Microphallidae). *Tul. Stud. in Zool. and Bot.*, 15(3):81-105.
- Buckner, R. L., R. M. Overstreet, and R. W. Heard. 1978. Intermediate Hosts for Tegorhynchus furcatus and Dollfusentis chandleri (Acanthocephala). *Proc. Helm. Soc. Wash.* 45(2):195-201.
- Bullock, W. L. 1957. The Acanthocephalan Parasites of the Fishes of the Texas Coast. *Publ. Inst. Mar. Sci.* 4(2):278-283.
- Bullock, W. L. 1969. Acanthocephala in Problems in Systematics of Parasites. *Univ. Park Press Balt.* 131 pp.
- Bullock, W. L. and E. Mateo. 1970. A reconsideration of the acanthocephalan genera: Telosentis, Illiosentis, and Tegorhynchus on the basis of type specimens. *Proc. Second Int. Congr. Parasitol.*, Part 1, *J. Parasitol.* 56:41-42.
- Cable, R. M., R. S. Connor and J. W. Balling. 1960. Digenetic trematodes of Puerto Rican shore birds. *Sci. Survey Porto Rico and Virgin Isl. N.Y. Acad. Sci.*, 17:187-254.
- Cable, R. M. and J. Linderoth. 1963. Taxonomy of some Acanthocephala from marine fishes with reference to species from Curacao, N.A., and Jamaica, W.I. *J. Parasit.* 49:706-716.
- Causey, D. 1953. Parasitic copepods from Grand Isle, Louisiana. *Occasional Papers, Marine Laboratory, Louisiana State University*, 7, Baton Rouge, Louisiana, USA.
- Chandler, A. C. 1934. A revision of the genus Rhadinorhynchus (Acanthocephala) with descriptions of new genera and species. *Parasit.* 26:351-358.
- Chandler, A. C. 1935. Parasites of fishes in Galveston Bay. *Proc. U.S. Nat. Mus.* 83:123-157.
- Chandler, A. C. 1942. Some cestodes from Florida sharks. *Proc. U.S. Natl. Mus.* 92:25-31.
- Chandler, A. C. 1954. Acanthocephala (in Gulf of Mexico, its origin, waters and marine life). *Fish. Bull.* (89) U.S. Fish and Wildlife Serv., 355.

- Chabanaud, P. 1929. La taxonomie la morphologie et la bionomie des Soleides du genre Pegusa. Ann. Inst. Oceanogr., 7(6):215-226.
- Chao, L. N. 1976. Aspects of systematics, morphology, life history and feeding of western Atlantic Sciaenidae (Pisces: Perciformes). Ph.D. Thesis, College of William and Mary, Williamsburg, Va., 342 p. [Diss. Abstr. 37(5):2105-B (Order No. 76-25, 354).]
- Chao, L. N. 1978. A Basis for Classifying Western Atlantic Sciaenidae (Teleostei: Perciformes) NOAA Tech. Rep., NMFS Tech. Circ. 415: 1-64.
- Chao, L. N. and J. A. Musick. 1977. Life history, feeding habits and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull., U.S. 75:657-702.
- Cheng, T. C. 1973. General Parasitology. Academic Press, N.Y. and London. 965 pp.
- Cloutman, D. G. 1975. Parasite community structure of large mouth bass, warmouth, and bluegill in Lake Fort Smith, Arkansas. Trans. Amer. Fish. Soc. 104(2):277-283.
- Cole, L. C. 1949. The measurement of interspecific association. Ecology 30:411-424.
- Cole, L. C. 1957. The Measurement of Partial Interspecific Association. Ecology 38(2):226-233.
- Cressey, R. F. 1972. The genus Argulus (Crustacea: Branchiura) of the U.S. Biota of Freshwater Ecosystems Identification Manual, No. 2:1-11.
- Crowcroft, P. W. 1946. A description of Sterrhurus macrorchis n. sp. with notes on the taxonomy of the genus Sterrhurus Looss (Trematoda-Hemiuridae). Pap. and Proc. Roy. Soc. Tasm. 1945, 39.47.
- Cuvier, G. 1830. In G. Cuvier and A. Valenciennes. Histoire naturelle des poissons. F. G. Levrault, Paris. Vol. 5, 499 pp.
- Darnell, R. M. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, and estuarine community. Publ. Inst. Mar. Sci., Univ. Tex. 5:353-416.
- Deturk, W. E. 1940. Parasites and commensals of some crabs of Beaufort, North Carolina. Ph.D. Thesis, Duke University.
- Diaz, A. and C. A. Johnson, III. 1974. The effect of season and salinity on the distribution of parasites of estuarine fishes from North Carolina. ASB Bull. 21:15.

- Dillon, W. A. and W. J. Hargis, Jr. 1966. Procedures for collection and study of Monogenetic trematodes. VIMS Parasit. Sec. Rep. No. 1.
- Dogiel, V. A. 1970. Ecology of the Parasites of Freshwater Fishes. In Parasitology of Fishes, Dogiel, V. A., G. K. Petrusheuski, and Yu. I. Polyanski (Eds.), T.F.H. Publications, N.J. 384 pp.
- Eckmann, F. 1932. Beitrage zur Kenntniss der Trematodenfamilie Bucephalidae. Zeitschr. Parasitenk., 5(1):94-111.
- Edwards, S. R. and F. M. Nahhas. 1968. Some endoparasites of fishes from the Sacramento-San Joaquin Delta, Calif. Calif. Fish and Game 54(4):247-256.
- Esch, G. W., J. W. Gibbons and J. E. Bourgue. 1979. Species diversity of helminth parasites in Chrysemys S. Scripta from a variety of habitats in South Carolina. J. Parasit. 65(4):633-638.
- Freeman, R. S. 1973. Ontogeny of cestodes and its bearing on their phylogeny and systematics, 481-557. In Ben Dawes (Ed.), Adv. in Parasit., Vol. II. Academic Press, New York.
- Gallaway, B. J. and K. Strawn. 1974. Seasonal abundance and distribution of marine fishes at a hot-water discharge in Galveston Bay, Texas. Contrib. Mar. Sci., Univ. Tex. 18:71-137.
- Gibson, D. I. 1972. Flounder Parasites as Biological Tags. J. Fish. Biol. 4:1-9.
- Golvan, Y. J. 1969. Systematigues des acanthocephales (acanthocophala Rulldolph, 1801): premiere partie l'ordre des Palaeoacanthocephala Meyer 1931. Mem. Mus. Nat. Hist. Nat. Sev. A. Zool. 57:1-373.
- Greig-Smith, P. 1964. Quantitative Plant Ecology. Butterworth and Co., London. 256 pp.
- Gunter, G. 1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci., Univ. Tex. 1:1-190.
- Hanson, D. J. 1969. Food, growth, migration, reproduction, and abundance of pinfish, Lagodon rhomboides, and Atlantic croaker, Micropogon undulatus, near Pensacola, Florida 1963-65. U.S. Fish. Wildl. Serv. Fish. Bull. 68(1):135-146.
- Hargis, W. J. 1956. Monogenetic trematodes of Gulf of Mexico Fishes. The superfamily Diclidophoroidea Price, 1936 (continued). Proc. Helm. Soc. Wash. 23, 5-13.
- Haven, D. S. 1954. Croakers. Va. Comm. Fish. 54th and 55th Annu. Rep. 1952-1953, 49-53.
- Haven, D. S. 1957. Distribution, growth, and availability of juvenile croaker, Micropogon undulatus, in Virginia. Ecology 38(1):88-97.

- Haven, D. S. 1959. Migration of the croaker, Micropogon undulatus. Copeia (1):25-30.
- Hendrix, S. S. and R. M. Overstreet. 1977. Marine Aspidogastriids (Trematoda) from fishes in the Northern Gulf of Mexico. J. Parasit. 63(5):810-817.
- Hildebrand, S. F. and W. C. Schroeder. 1928. Fishes of the Chesapeake Bay. Bull. U.S. Bur. Fish. 43, Pt. 1, 366 pp.
- Hildebrand, S. F. and L. E. Cable. 1930. Development and life history of fourteen teleostea fishes at Beaufort, N.C. Bull. U.S. Bur. Fish. 46:384-488.
- Hirsch, R. P. and H. T. Gier. 1974. Multiple species infections of intestinal helminths in Kansas coyotes. J. Parasit. 60(4):650-653.
- Ho, J. S. 1977. Marine flora and fauna of the northeastern U.S. Copepoda: Lernaepodidae and Sphriidae. NOAA Tech. Rep. NMFS Circ. 406.
- Hoffman, G. L. 1967. Parasites of North American Freshwater fishes. Univ. Calif. Press 486 p.
- Holmes, J. C. and R. Podesta. 1968. The helminths of wolves and coyotes from the forested regions of Alberta. Can. J. Zool. 46:1193-1204.
- Hobbs, R. P. 1979. Interspecific interactions among gastrointestinal helminths in Pikas of North America. Amer. Midl. Nat. 103(1):15-25.
- Hopkins, S. H. 1941a. New genera and species of the family Monorchidae (trematoda) with a discussion of the excretory system. J. Parasit. 27(5):395-407.
- Hopkins, S. H. 1941b. The excretory systems of Helicometra and Cymbophallus (trematoda) with remarks on their relationships. Trans. Amer. Micro. Soc. 60:41-44.
- Hopkins, S. H. 1958. Trematode parasites of Donax variabilis at Mustang Island, Texas. Publ. Inst. Mar. Sci., Univ. Tex. 5:301-311.
- Huehner, M. K. and F. J. Etges. 1977. The Life Cycle and Development of Aspidogaster conchicola in the Snails, Viviparus malleatus and Goniobasis livescens. J. Parasit. 63(4):669-674.
- Huizinga, H. W. and A. J. Haley. 1962. Occurrence of the Acanthacephalan parasite Telosentis tenicornis, in the spot, Leiostomus xanthurus, in the Chesapeake Bay. Ches. Sci. 3(1):35-42.



- Hunninen, A. V. and R. M. Cable. 1941. Studies on the life history of Anisoporus manter, Hunninen et Cable 1940 (Trematoda: Allocreadiidae). Biol. Bull. 80(3):415-428.
- Jones, D. O. 1943. The anatomy of three digenetic trematodes, Skrjabiniella aculeatus (Odhner), Lecithochirium rutoviride (Rud.) and Sterrhurus fusiformis (Luke) from Conger conger. Linn. Idib. 35:40-57.
- Jordan, D. S. 1917. The genera of fishes and a classification of fishes. Stanford Univ. Press, Stanford, 800 pp.
- Joseph, E. B. 1972. The status of sciaenid stocks of the Middle Atlantic coast. Ches. Sci. 13(2):87-100.
- Joy, J. E. 1971. Spirocamallanus pereirai (Nematoda: Camallanidae) from the croaker, Micropogon undulatus, in Texas. J. Parasit. 57(2):390.
- Joy, J. E. 1972. New locality records for Diplomonorchis leiostomi Hopkins, 1941 (Trematoda, Digenea) and Macrovalvitrematoides micropogoni (Pearse, 1949) (Trematoda, Monogenea) with notes on their geographical distributions. Tex. J. Sci. 28(4):553-554.
- Joy, J. E. 1974. Incidence and intensity of Spirocamallanus pereirai (Nematoda: Camallanidae) infestations in the croaker, Micropogon undulatus (Linnaeus) and spot, Leiostomus xanthurus Lacepede, from Texas. Contrib. Mar. Sci. 18:1-6.
- Kabata, Z. 1963. Parasites as biological tags. Int. Comm. N.W. Atl. Fish., Spec. Pub. No. 4:31-37.
- Kingston, N., W. A. Dillon and W. J. Hargis, Jr. 1969. Studies on larval monogenea of fishes from the Chesapeake Bay area. Part 1. J. Parasit. 55(3):544-558.
- Lagler, K. F. 1952. Freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa 360 pp.
- Lambert, J. M. and W. T. Williams. 1962. Multivariate methods in plant ecology. IV. Nodal Analysis. J. Ecol. 5:775-802.
- Lance, G. N. and W. T. Williams. 1966. A generalized sorting strategy for computer classifications. Nature 212:218.
- Lance, G. N. and W. T. Williams. 1967. A general theory of classificatory sorting strategies. I. Hierarchical Systems. Comput. J. 9:373-380.
- Lawler, A. R. and R. M. Overstreet. 1976. Absonifibula bychowski gen. et sp. n. (Monogenea: Absonifibulinae Subfam. N.) from the Atlantic croaker, Micropogon undulatus (L) from Mississippi, U.S.A. Institute of Biology and Pedology Far-East Science Centre Acad. of Sciences of the USSR - Studies on Monogeneans. Vladivostok 1976 34(137):83-91.

- Linton, E. 1889. Notes on Entozoa of marine fishes of New England with descriptions on several new species. Rep. U.S. Commissioner for 1886. Part 4, 453-511.
- Linton, E. 1891. Notes on Entozoa of marine fishes, with descriptions of new species. Part 3. Rep. U.S. Commissioner of Fish and Fisheries for 1889, 523-542.
- Linton, E. 1905. Parasites of fishes of Beaufort, North Carolina. Bull. U.S. Bur. Fish. (1904). 24:321-428.
- Linton, E. 1907. Notes on parasites of Bermuda fishes. Proc. U.S. Nat. Mus. 33:85-126.
- Linton, E. 1932. On the taxonomic position of Echinorhynchus sagittifer Linton. Sci. n.s. (1965), Vol. 76, p. 193.
- Looss, A. 1907. Beitrage zur Systematik der Distomen. Zool. Jahr. Syst. 26, 63-180.
- Lubieniecki, B. 1977. The plerocercus of Grillotia erinaceus as a biological tag for haddock Melanogrammus aeglefinus in the north sea and northeast Atlantic. J. Fish. Biol. 11, 555-565.
- MacCallum, G. A. 1921. Studies in helminthology. Part 1. Trematodes. Part 2. Cestodes. Part 3. Nematodes. Zoopathologica 1:135-284.
- MacKenzie, K. 1975. Parasites trace herring migrations. Scott. Fish. Bull. (42):22-26.
- Manter, H. W. 1931. Some digenetic trematodes of marine fishes of Beaufort, North Carolina. Parasit. 23(3):396-411.
- Manter, H. W. 1940. Digenetic trematodes of fishes from the Galapagos Islands and the neighboring Pacific. Allan Hancock Pac. Exped., 2(14):323-497.
- Manter, H. W. 1947. The digenetic trematodes of marine fishes of Tortugas, Florida. Amer. Midl. Nat. 38(2):257-416.
- Margolis, L. 1965. Parasites as an auxiliary source of information about the biology of Pacific salmon (Genus Oncorhynchus). J. Fish. Res. Bd. Can. 22(6):1387-1395.
- Markle, D. F. 1976. The seasonality of availability and movements of fishes in the Channel of the York River, Virginia. Ches. Sci. Vol. 17, No. 1:50-55.
- Markov, G. S. 1958. Physiology of Fish Parasites. In Parasitology of Fishes. Dogiel, V. A., G. K. Petrushevski, and Yu. J. Polyanski (Eds.). T.F.H. Publications. N.J. 384 pp.

- Martin, W. E. 1938. Studies on Trematodes of Woods Hole; The Life Cycle of Lepocreadium setiferoides (Miller and Northrup), Allocreadiidae, and the description of Cercaria cumingiae n. sp. Biol. Bull. 75, 463-474.
- Martin, W. E. 1939. Studies on the trematodes of Woods Hole. II. The life cycle of Stephanostomum tenue (Linton) Biol. Bull. 77(1):65-73.
- Massmann, W. H. 1954. Marine fishes in fresh and brackish waters of Virginia rivers. Ecology 35:75-78.
- Massmann, W. H. and A. L. Pacheco. 1960. Disappearance of young Atlantic croakers from the York River. Trans. Am. Fish. Soc. 89:154-159.
- Meehan, O. L. 1940. A review of the parasitic crustacea of the genus Argulus in the collections of the U.S. National Museum. Proc. U.S. Natl. Mus. 88(3087):459-522.
- Mercias, C. E. 1978. The eye lens weight technique in aging of the Atlantic croaker, Micropogon undulatus. Gulf Res. Reports 6(1):71-73.
- Meyer, A. 1932. Acanthocephala in Bronn's Klassen and Ordnungen des Tierreichs. Leipzig. 582 pp.
- Meyer, M. C. 1954. The larger animal parasites of the freshwater fishes of Maine. Maine Dept. Inland Fish and Game, Fish. Res. and Mgt. Div. Bull. (1):1-92.
- Miller, R. S. 1967. Pattern and process in competition. Adv. Ecol. Res. 4:1-74.
- Moore, J. P. 1898. The leeches of the U.S. National Museum. Proc. U.S. Natl. Mus., 21:543-563.
- Mulligan, W. 1972. The effect of helminthic infections on the protein metabolism of the host. Proc. of the Nutrition Soc. 31(1):47-51.
- Nahhas, F. M. and R. M. Cable. 1964. Digenetic and aspidogastroid trematodes from marine fishes of Curacao and Jamaica. Tulane Stud. Zool., 11:167-228.
- Nahhas, F. M. and E. C. Powell. 1965. Monorchidae (Trematodes) from fishes of Apalachee Bay, Gulf of Mexico. J. Parasit. 51(1):16-20.
- Nicholson, A. J. 1954. An outline of the dynamics of animal populations. Aust. J. Zool. 2:9-65.
- Noble, E. R. and G. A. Noble. 1971. Parasitology - The Biology of Animal Parasites. Lea and Febiger, Philadelphia. 617 pp.

- Norris, D. E. and R. M. Overstreet. 1975. Thynnascaris reliquens sp. n. and T. habena (Linton, 1900) (Nematoda: Ascaridoidea) from fishes in the northern Gulf of Mexico and eastern U.S. seaboard. J. Parasit. 61(2):330-336.
- Odum, E. P. 1971. Fundamentals of Ecology, W. B. Saunders Company, Philadelphia. 574 pp.
- O'Rourke, A. F. 1949. Preliminary survey of the macroscopic parasites of food fishes in the vicinity of Solomons, Md. J. Tenn. Acad. Sci. 24-25:134.
- Overstreet, R. M. 1969. Ecological aspects of the acanthocephalan Dollfusentis chandleri, Golvan 1969 in an estuarine fish. Amer. Soc. Parasit., Abst. 239.
- Overstreet, R. M. 1971. Metadena spectandra Travassos, Freitas and Buhrnheim, 1967 (Digenea: Cryptogonimidae) in estuarine fishes from the Gulf of Mexico. Proc. of Helm. Soc. of Wash. 38(20): 156-158.
- Overstreet, R. M. 1972. Digenetic Trematodes of the Chesapeake Bay. Ches. Sci., Vol. 13, Supplement:106-107.
- Overstreet, R. M. 1973. Some species of Lecithaster Lulle 1901 (Digenea: Hemiuridae) and related genera from fishes in the Northern Gulf of Mexico. Trans. Amer. Micro. Soc. 92(2):231-240.
- Overstreet, R. M. 1977. Poecilancistrum caryophyllum and other trypanorhynch cestode pleurocercoids from the musculature of Cynoscion nebulosus and other sciaenid fishes in the Gulf of Mexico. J. Parasit. 63(5):145-152.
- Overstreet, R. M. and R. W. Heard. 1978. Food of the Atlantic croaker, Micropogonias undulatus from Mississippi Sound and the Gulf of Mexico. Gulf Res. Rep. 6(2):145-152.
- Paperna, I. and D. E. Zwerner. 1976. Parasites and diseases of striped bass, Morone saxatilis from the lower Chesapeake Bay. J. Fish. Biol. 9, 67-287.
- Parker, J. C. 1971. The biology of the Spot, Leiostomus xanthurus Lacepede and Atlantic croaker, Micropogon undulatus (Linnaeus), in two Gulf of Mexico nursery areas. Sea Grant Publication No. TAMU-SG-210, Tex. A&M Univ., College Station. 182 pp.
- Pavlovski, E. N. 1934. Organism as Environment. Priroda 1.
- Pearse, A. S. 1947. Parasitic copepods from Beaufort, North Carolina. J. Elisha Mitchell Sci. Soc. 63(1):1-16.
- Pearse, A. S. 1949. Observation on flatworms and nemerteans collected at Beaufort, N.C. Proc. U.S. Natl. Mus. 100(3255):24-38.

- Pearson, J. C. 1929. Natural history and conservation of redbfish and other commercial sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129-214.
- Pearson, J. C. 1932. Winter trawl fishery off the Virginia and North Carolina coasts. U.S. Bur. Fish., Invest. Rep. 10, 31 p.
- Pianka, R. M. 1976. Competition and niche theory in theoretical ecology. R. M. Man, Editor. W. B. Saunders Co., Phil., Pa. 317 pp.
- Polyanski, Yu. I. 1958. Ecology of Parasites of Marine Fishes. In Parasitology of Fishes Dogiel, V. A., G. K. Petrushevski, and Yu. J. Polyanski (Eds.). T.F.H. Publications, N.J. 384 pp.
- Prakash, A. and J. R. Adams. 1960. A histopathological study of intestinal lesions induced by Echinorhynchus lageniformis (Acanthocephala Echinorhynchidae) in the starry flounder. Can. J. Zool. 38:895-897.
- Prevot, T. and S. Deblock. 1970. Key to the known species of Megalophallus. Annls. Parasit. Hum. Comp., 45(2):213-222.
- Pritchard, D. W. 1967. Observations of circulation in coastal plain estuaries. In Estuaries pp. 37-44 (Lauff, G. H., Ed.). Amer. Assoc. Adv. Sci., Publ. 83.
- Putz, R. E. 1972. Cryptobia cataractae sp. n. (Kinetoplastida: Cryptobiidae), a haemoflagellate of some cyprinid fishes of West Virginia. Proc. Helm. Soc. Wash., 39(1);18-22.
- Raney, E. C. and W. H. Massmann. 1953. The fishes of the tidewater section of the Pamunkey River, Virginia. J. Wash. Acad. Sci. 43:424-432.
- Richardson, H. 1905. Isopods of North America. Bull. U.S. Natl. Mus. No. 54:263-265.
- Roelofs, E. W. 1954. Food studies of young sciaenids fishes Micropogon and Leiostomus from North Carolina. Copeia 2:151-153.
- Sanders, H. L. 1968. Marine benthic diversity: A comparative study. The American Naturalist. 102(925):259-270.
- Saunders, D. C. 1964. Blood parasites of marine fish of southwest Florida, including a new haemogregarine from the menhaden, Brevoortia tryannus (Latrobe). Trans. Amer. Micro. Soc., 83:218-225.
- Sawyer, R. T. and N. A. Chamberlain. 1972. A new species of marine leech (Annelida: Hirudinea) from South Carolina, parasitic on the Atlantic menhaden, Brevoortia tyrannus. Biol. Bull. 142(3):470-479.

- Sawyer, R. T. and D. L. Hammond. 1973. Observations on the marine leech Calliobdella carolinensis (Hirndinea: Piscicolidae), epizootic on the Atlantic Menhaden. Biol. Bull. 145:373-388.
- Sawyer, R. T., A. R. Lawler and R. M. Overstreet. 1975. Marine leeches of the Eastern U.S. and the Gulf of Mexico with a key to the species. J. Nat. Hist. 9:633-667.
- Schell, S. C. 1970. How to Know the Trematodes. Wm. C. Brown, Dubuque, Iowa. 366 pp.
- Seamster, A. and L. H. Monaco. 1956. Rhamnocercus. A new species of Rhaminocercinae. Am. Midl. Nat. 55(1):180-183.
- Simpson, E. H. 1949. Measurement of Diversity. Nature, 163:688.
- Short, R. B. 1953. A new blood fluke, Cardicola laruei N.G., n. sp., (Aporocotylidae) from marine fishes. J. Parasit. 39(3):304-309.
- Sindermann, C. J. 1961. Parasitological tags for redfish of the western North Atlantic. ICNAF Spec. Publ. 3.
- Sindermann, C. J. 1970. Principal Diseases of Marine Fish and Shellfish. Academic Press, N.Y. and London. 368 p.
- Sagath, P. H. and R. R. Sokal. 1973. Numerical taxonomy, the principles and practice of numerical classification. Freeman, San Francisco, 573 pp.
- Snieszko, S. F. 1973. Recent advances in scientific knowledge and developments pertaining to diseases of fishes. Adv. Vet. Sci. and Compar. Med. 17:291-314.
- Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co. 716 pp.
- Sogandares-Bernal, F. 1955. Some helminth parasites of fresh and brackish water fishes from Louisiana and Panama. J. Parasit. 41:587-594.
- Sogandares-Bernal, F. and R. F. Hutton. 1959. Studies on Helminth parasites from the Coast of Florida III. Digenetic trematodes of Marine Fishes from Tampa and Boca Ciega Bays. J. Parasit. 45(3): 337-346.
- Sogandares-Bernal, F. and R. F. Hutton. 1960. The status of some marine species of Lepocreadium Stossich 1904 (Trematoda: Lepocreadiidae) from the North American Atlantic. Librohomenaje Eduardo Caballero y C., 275-283.
- Sparks, A. K. 1958. Some digenetic trematodes of fishes of Grand Isle, Louisiana. Proc. La. Acad. Sci. 20:71-82.

- Sparks, A. K. 1960. Some aspects of the zoogeography of the digenetic trematodes of shallow-water fishes of the Gulf of Mexico. Lib. Hom. E. Caballero y. C.:285-298.
- Sparks, A. K. and V. E. Thatcher. 1956. A new species of Stephanostomum (Trematoda, Acanthocolipidae) from Marine Fishes of the Northern Gulf of Mexico. Trans. Amer. Micro. Soc. 77(3):287-290.
- Stephenson, W. 1973. The use of computers in classifying marine bottom communities. In R. Fraser (Comp.) Oceanography of the South Pacific. N. Z. Nat. Comm. for UNESCO, Wellington. 463-473.
- Stickney, R. R. and S. E. Shumway. 1974. Occurrence of cellulase activity in the stomachs of fishes. J. Fish. Biol. 6:779-790.
- Stickney, R. R., G. L. Taylor and D. B. White. 1975. Food habits of five species of young Southeastern United States estuarine Sciaenidae. Ches. Sci. 16(2):104-114.
- Stone, J. E. and D. Pence. 1978. Ecology of helminth parasitism in the bobcat from West Texas. J. Parasit. 64(2):295-302.
- Stunkard, H. W. 1960. Problems of the generic and specific determination of digenetic trematodes with special reference to the genus Microphallus Ward, 1901. Lib. Homenaje Dr. E. Caballero y C. Mexico, D. F., 299-309.
- Stunkard, H. W. 1969. Lepocreadium areolatum (Linton, 1900) N. Comb., syn. Distomum areolatum Rudolphi of Linton, 1900 (Trematoda: Digenea). Trans. Amer. Micro. Soc. 88(1):78-84.
- Stunkard, H. W. 1972. Observations on the morphology and life history of the digenetic trematode, Lepocreadium setiferoides. Biol. Bull. 142:326-334.
- Suriano, D. M. 1966. Estudio de la fauna parasitaria de Micropogon opercularis en relacion con problemas zoogeográficos del Atlantico Sur. Com. Mus. Argent. Cier. Nat. "B. Rivadavia" 1(3):31-47.
- Suriano, D. M. 1975. Systematica, Biologia y Microecologia de tres Monogenea, polyopisthocotylea parasitos de las Barnquias de Micropogon opercularis (Quoy y Gaimard) Y umbrina Canosai Berg (Pisces, Sciaenidae) del Oceano Atlantico Sudoccidental. Physis Secc. A. Buenos Aires. 34, 88:147-163.
- Suttkus, R. D. 1955. Seasonal movements and growth of the Atlantic croaker (Micropogon undulatus) along the east Louisiana coast. Proc. Gulf Carib. Fish. Inst. Seventh Annu. Sess., 151-158.
- Tate, M. W. and R. C. Clelland. 1957. Nonparametric and short cut statistics. Interstate Printers and Publishers, Inc. Danville, Illinois. 171 pp.

- Tarwid, K. 1960. Szacowanie zbieznoscinisz ekologicznych qatunkow droga oceny prawelopodobienstwa spotykania sie ich w polowach. Ekol. Pol. Ser. B, 6:115-130.
- Tuff, D. W. and D. G. Huffman. 1977. Index to the genera of hosts in Yamaguti's systema Helminthum, Tex. J. Sci, 28(1-4):161-191.
- VanCleave, H. J. 1918. Acanthocephala of the subfamily Rhadinorhynchinae from American fish. J. Parasit. 5:17-24.
- VanCleave, H. J. 1923. Telesentis, a new genus of Acanthocephala from southern Europe. J. Parasit. 9:174-175.
- VanCleave, H. J. 1947. On the occurrence of the Acanthocephalan genus Telosentis in North America. J. Parasit. 33(2):123-133.
- VanCleave, H. J. and D. R. Lincicome. 1940. A reconsideration of the acanthocephalan family Rhadinorhynchidae. J. Parasit. 33:17.
- VanCleave, H. J. and J. A. Ross. 1947. Use of trisodium phosphate in microscopical technic. Science 106(2748):194.
- Venard, C. F. and J. H. Warfel. 1947. Some effects of Acanthocephalan on the large-mouthed black bass. J. Parasitol. 33:17.
- Verrill, A. E. 1872. Description of North American leeches. Am. J. Sci., 3:126-139.
- Wallace, D. H. 1940. Sexual development of the croaker, Micropogon undulatus, and distribution of early stages in Chesapeake Bay. Trans. Amer. Fish. Soc. 69:475-482.
- Wardle, R. A. and J. A. McLeod. 1952. The Zoology of Tapeworms. Univ. of Minn. Press, 780 pp.
- Wass, M. L. (Compiler). 1972. A checklist of the biota of lower Chesapeake Bay. Virginia Inst. Mar. Sci., Spec. Sci. Rep., No. 65:1-290.
- Welsh, W. W. and C. M. Breder. 1923. Contributions to the life histories of Sciaenidae of the Eastern U.S. Coast. Bull. U.S. Bur. Fish. 39:141-201.
- Westrheim, S. J. and W. E. Ricker. 1978. Bias in using an age-length key to estimate age-frequency distributions. J. Fish. Res. Bd. Can. 35:184-189.
- White, M. L. and M. E. Chittenden. 1977. Age determination, reproduction and population dynamics of the Atlantic croaker, Micropogonias undulatus. Fish. Bull. 75(1):109-123.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities. Science 147:250-260.



- Wicklen, J. H. von. 1946. The trematode genus Opecoeloides and related genera, with a description of Opecoeloides polynemi n. sp. J. Parasit. 33(2):156-162.
- Wilhm, J. L. and T. C. Dorris, 1968. Biological parameters for water quality criteria. Bioscience 18(6):477-481.
- Williams, W. T. and J. M. Lambert, 1961. Nodal analysis of associated populations. Nature 191:202.
- Williams, W. T. 1971. Principles of clustering. Ann. Rev. Ecol. Syst. 2:303-326.
- Wilson, C. B. 1944. Parasitic copepods in the U.S. National Museum. Proc. U.S. Natl. Mus., 94(3177):529-582.
- Wojcik, F. 1978. Temperature-induced croaker mortality. Coastal Oceanography and Climatology News 1(1):5.
- Wood, R. A. and J. D. Mizelle. 1957. Studies on monogenetic trematodes XII North American Gyrodactylinae, Dactylogyrynae and a new host record for Urocleidus dispar (Mueller, 1936). Amer. Midl. Nat. 57, 183-202.
- Yamaguti, S. 1934. Studies on the helminthum of Japan. Part 4. Cestodes of fishes. Japn. J. Zool. 6, 1-112.
- Yamaguti, S. 1958. Systema Helminthum. Vol. I, Parts 1 & 2. Digenetic Trematodes. Interscience Publishers Inc., N.Y. and London, 1575 pp.
- Yamaguti, S. 1959. Systema Helminthum. Vol. II. Cestodes. Interscience Publishers Inc., N.Y. and London, 860 pp.
- Yamaguti, S. 1961. Systema Helminthum. Vol. III. Parts 1 and 2. Nematodes. Interscience Publishers Inc., N.Y. and London, 1261 pp.
- Yamaguti, S. 1963a. Systema Helminthum. Vol. IV. Monogenea and Aspidocotylea. Interscience Publishers Inc., N.Y. and London, 697 pp.
- Yamaguti, S. 1963b. Systema Helminthum. Vol. V. Acanthocephala. Interscience Publishers Inc., N.Y. and London, 423 pp.
- Yamaguti, S. 1975. A Synoptical Review of Life Histories of Digenetic Trematodes of Vertebrates. Keigaku Publ. Co., Tokyo, Japan. 800 pp.

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